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# Growth and distribution of Populus trichocarpa on an alluvial flood plain in northwestern Montana

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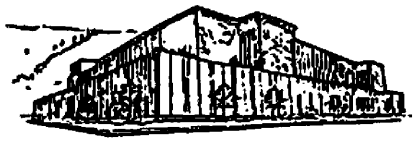

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# Growth and Distribution of *Populus trichocarpa* on an Alluvial Flood Plain in Northwestern Montana

By

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for the degree of Master of Science

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Growth and distribution of *Populus trichocarpa* on an alluvial flood plain in Northwestern Montana

Advisor: Jack A. Stanford

## Abstract

Interstitial flow within floodplain aquifers has been shown to influence fish spawning, benthic assemblages, and algal productivity. However, little is known of the effects of subsurface flow on the distribution and productivity of floodplain forests. This study, conducted on a flood plain of the Middle Fork of the Flathead River in Montana, tested the hypothesis that regional upwelling of groundwater increases the growth of black cottonwood, *Populus trichocarpa,* the dominant riparian tree species. Indices of growth rate determined from radial measures from tree rings were calculated for 32 plots. Plot growth rates were compared between losing and gaining reaches of the flood plain. Site variables, such as stand age and elevation above base flow, were spatially related to channel migrations and flood history as documented over time through aerial photographs and discharge records. Additionally, a soil protein thought to contribute to soil stability, nutrient retention, and plant growth, was quantified in plot soils.

Cottonwood growth and distribution were most influenced by variations in groundwater availability as related to topographic differences between the losing and gaining reaches. Over the growing season, water table elevation dropped 80 cm lower in the losing reach compared to the gaining reach. Cottonwood growth rates were negatively correlated with the decrease in water table elevation. In the gaining reach, radial growth of cottonwoods was approximately 35% greater than cottonwood growth in the losing reach. Depth to ground water and depth to coarse material explained most of the variance in growth between plots, based upon stepwise multiple linear regressions. Tree establishment was associated with the largest floods during the 60-year retrospective analysis of aerial photos. In the losing reach, cottonwood trees colonized adjacent to historic river channels, where zones of preferential groundwater flow (paleochannels) provided increased soil moisture and perhaps greater nutrients. In the gaining reach, significantly greater concentrations of protein were present.

Interstitial flow influenced the productivity of cottonwood trees at Nyack Flood Plain, which supports the conclusion from other research on this flood plain that subsurface water flux drives ecosystem structure and function and has profound implications for management.

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# Chapter 1

## Overview of Cottonwood Ecology

Cottonwood forests occupy ecotones between terrestrial and aquatic ecosystems (Gregory et al. 1991) and are critical biological and physical components of river ecosystems throughout the Northern Hemisphere. Cottonwood trees act as ecosystem engineers (Jones et al. 1994) by depositing wood into river channels (Abbe and Montgomery 1996), contributing to island formation and soil stabilization (Leopold and Wolman 1957, Everitt 1968, Kollmann 1999), and providing wildlife habitat and forage (Carothers et al. 1974, Finch and Ruggiero 1993). To exert these influences, cottonwoods depend on river conditions that support tree establishment and growth. Fluvial disturbances, such as floods to scour competing vegetation and to deposit sediments are necessary for cottonwood recruitment (Bradley and Smith 1986, Braatne et al. 1996). Cottonwoods also require access to ground water for establishment (Segelquist et al. 1993, Mahoney and Rood 1998, Cooper et al. 1999) and survival (Busch and Smith 1995, Scott et al. 1999). Continued alterations of river landscapes by humans that interfere with the establishment and growth of cottonwoods, such as damming and cattle grazing, threaten cottonwood forests. This chapter reviews how cottonwoods interact with the environment, discusses components of cottonwood life history that are related to fluvial events, and discusses of how legacies of rivers can be inferred from cottonwoods.

### *Importance of cottonwoods in river landscapes*

Cottonwood trees affect alluvial rivers by altering the physical environment of river systems, thus acting as ecosystem engineers. Jones et al. (1994) defined an

ecosystem engineer as "an organism that directly or indirectly modulates the availability of resources to other species, by causing physical state changes in biotic or abiotic materials." For example, cottonwoods engineer ecosystems by depositing wood into rivers. When boles or branches or cottonwoods are deposited on a flood plain, fine sediments accumulate on the downstream end of the wood (Fetherston et al. 1995, Abbe and Montgomery 1996). The wood jam leads to the formations of floodplain surfaces (Fetherston et al. 1995) that are later colonized by plants (Kollmann 1999), as well as contributes to channel avulsions. Furthermore, cottonwood seedlings growing on exposed bars screen deposits of silt and fine sand. Sediment trapping and plant establishment lead to expansion of the bar and formation of islands or connected landmasses (Leopold and Wolman 1957, Everitt 1968). As the size of the landmass increases through stabilization by vegetation, the river channel cuts laterally and vertically, thus causing the channel to divide and move (Leopold and Wolman 1957). By providing shade, trapping fine sediments, and raising the ground elevation relative to the river channel for flood protection, cottonwoods appear to facilitate the establishment of plants less tolerant to flooding and direct sunlight.

The forest and habitat provided by cottonwood trees benefit wildlife communities by offering forage, cover, and reproduction sites for birds and mammals (reviewed in Finch and Ruggiero 1993). In north-central Arizona, Carothers et al. (1974) found that homogeneous cottonwood stands supported more species and denser populations of nesting birds compared to mixed deciduous stands. Cottonwood gallery forests contribute large leaf deposits into rivers (Stanford and Ward 1986). The leachate from leaves provides organic matter that supports benthic microbial communities and aquatic

invertebrates (Cummins 1974, Cummins et al. 1983, Triska et al. 1989). Cottonwood forests are also wintering and calving grounds for deer and elk. Additionally, bears use old, hollow cottonwoods as den sites. Cottonwood trees also provide forage and construction material for beaver (*Castor canadensis*) (McGinley and Whitham 1985).

Cottonwoods alter community structure through the gene expression within the trees (Whitham et al. 1999). Waltz and Whitham (1997) measured developmental changes between juvenile and mature growth of cottonwood leaves and found that leaves from different positions on the tree varied in content of defensive chemicals. The chemical variation affected the distribution of aphids and beetles, which in turn altered arthropod communities. When a species of aphid that fed on mature cottonwood shoots was removed, arthropod species richness decreased. Conversely, when beetles that fed on juvenile shoots were removed, arthropod species richness and abundance increased. Another study found that browsing by beavers changed the leaf chemistry of cottonwoods. Martinsen et al. (1998) measured re-sprout growth from stumps and roots and discovered that re-sprout growth had twice the levels of defensive chemicals as normal juvenile growth. Phenolic glycosides, produced as a plant defense for herbivores, attracted beetles (*Chrysomela confluens*) that converted the chemical for use in the beetle's own defenses. The beetles also acquired a nutritional source from the compounds through the release of glucose.

Though less studied, processes occurring in the rhizosphere of cottonwoods may engineer ecosystems. Jones et al. (1994) defined allogenic engineers as "organisms that change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means." For example, mycorrhizal fungi on

roots of cottonwood trees (Vozzo and Hacskaylo 1974, Schultz et al. 1983, Brundrett et al. 1990) may influence the stability and nutrient stores in soils. Arbuscular mycorrhizae living in association with other plants have been found to produce a glycoprotein named glomalin (Wright and Upadhyaya 1996). Fungal glycoproteins, along with fungal and bacterial hyphae and plant polysaccharides, bind soil micro-aggregates into larger water-stable aggregates that give soil desirable properties (Tisdall et al. 1997, Wright and Upadhyaya 1998). Soil structure affects plant productivity because water-stable aggregates provide habitat for microorganisms that are important in the mobilization of nitrogen and phosphorous needed for plant nutrition, as well as increases water and nutrient retention, aeration, and erosion resistance (De Freitas et al. 1996, Andrade et al. 1998). Furthermore, the proteins themselves are comprised of carbon (Rillig et al. 1999), so soil proteins may provide a carbon source to floodplain food webs. The mycorrhizal fungi living on cottonwood and other riparian plant roots may have far-reaching influences on ecosystems in terms of soil stability and nutrient storage.

Additionally, cottonwoods may hydraulically lift water from deeper soil layers, thus increasing soil moisture to plants with shallower root systems. Hydraulic lift is a process by which water is absorbed by deep roots in moist soil and then moved through the roots where it is released in the upper soil profile (Richards and Caldwell 1987). Lab studies by Hanson and Dickson (1979) showed that poplar species transferred water between roots of neighboring seedlings, but field studies of hydraulic lift for cottonwoods are lacking. However, hydraulic lift has been documented for other species (Richards and Caldwell 1987, Caldwell and Richards 1989, Emerman and Dawson 1996).

*The genus Populus*

Relatives to aspens (*Populus* spp.) and willows (*Salix* spp.), cottonwoods belong to the family *Salicaceae*, a family distributed throughout the Northern Hemisphere. Members of the family are dioecious, produce flowers in catkins, and bear capsular seeds lacking endosperm and covered with long, white hairs. The genus comprises approximately 40 species divided among six sections, five of which occur in North America: The *Aigeiros* section contains *P. deltoides* (plains or eastern cottonwood) and *P. fremontii* (Fremont cottonwood); the *Tacamahaca* section contains *P. balsamifera* (balsam cottonwood), *P. trichocarpa* (black cottonwood), and *P. angustifolia* (narrowleaf cottonwood), and the *Populus* section contains *P. tremuloides* (aspen) (Eckenwalder 1996, Farmer 1996). Generally, members of the *Tacamahaca* section occupy sites of higher elevation compared to the *Aigeiros* section (Braatne et al. 1996). The prolific hybridization that occurs within the genera sometimes leads to difficulties in taxonomic classification. However, this hybridization also affects genetic structures that alter the surrounding community (Whitham et al. 1999).

*Cottonwood reproduction and early growth*

Cottonwoods reproduce sexually and asexually. Sexual reproduction permits cottonwoods to colonize new sites and promotes genetic diversity. Cottonwoods reach sexual maturity around 7-10 years (DeBell 1990) and typically live 100-200 years, but trees 200-300+ are recorded throughout their distribution (DeBell 1990, Zasada and Phipps 1990). Sexual reproduction is closely tied to peak river discharge. Trees flower from March-May as river stages begin to rise from snowmelt. Around the time of peak

discharge, cottonwoods release small (0.3 mg), cottony seeds that are dispersed by wind and water (Zasada and Phipps 1990). Seeds are viable for 1-2 weeks and germinate within 24 hours upon contact with moist, bare soils. Since the seeds lack endosperm, seedlings require access to water and sunlight for survival (reviewed in Braatne et al. 1996).

Root development is tied to the descending limb of the hydrograph and begins within 12 hours of germination. First, root hairs form, and within five days a primary root starts to grow. Radial roots also develop and grow 5-20 cm from the ground. From the radial roots, sinker roots descend more than 3 m into the soil (Pregitzer and Friend 1996). Roots grow rapidly, 0.5-1 cm/day (Mahoney and Rood 1998), leading to mature trees with root depths of 3-5+ m (Braatne et al. 1996). As the hydrograph declines, the roots develop to maintain contact with moist soils. If water levels drop faster than roots grow, the seedling dies. The dependence of the seedling on unvegetated soil and access to ground water make recruitment rare in relation to the number of seeds produced (Mahoney and Rood 1991, 1998). Generally, conditions conducive to recruitment occur once every 5 or 10 years on unregulated rivers (Mahoney and Rood 1998). On rivers without spring floods and sufficient groundwater reserves, decades may pass without recruitment. This lack of establishment is apparent in senescing stands of cottonwoods growing along rivers throughout the West (Bradley and Smith 1986, Rood and Heinze-Milne 1989).

Asexual reproduction also occurs in cottonwoods, particularly in the *Tacamahaca* section (Brayshaw 1965, Gom and Rood 1999). Cottonwoods may reproduce by suckering from roots, sprouting from stumps, or rooting from plant fragments. Root

suckering occurs on perimeters of established stands (Galloway and Worrall 1979) and on sites unfavorable to seedling establishment, such as on dry, sandy sites or frequently inundated sites (Krasny et al. 1988a&b). Stump sprouting follows beaver cutting, wind damage, sheering by water or ice, as well as girdling of young trees by voles and other rodents (M. Harner personal observations). Cottonwoods also reproduce via the rooting of plant fragments, such as twigs (Bessey 1901) that have been physically removed from the parent tree. The trees may shed fragments through cladopotosis, defined as "the physiological abscission of lateral twigs and branches with considerable secondary thickening" (Galloway and Worrall 1979). Through cladopotosis, cottonwoods drop twigs, usually about 5-10 cm long, most often in the fall. The twigs serve as propagules and either root near the parent tree, or are carried downstream (Galloway and Worrall 1979).

The ability to form adventitious roots (Krasny et al. 1988b), as well as to shift between sexual and asexual reproduction, affects the distribution of cottonwoods, aspen, and willow (Krasny et al. 1988a). Species that form adventitious roots, such as willow and some cottonwoods, can survive and grow in saturated soils. Krasny et al. (1988b) found that cottonwood and willows suckered from roots on floodplain sites, but aspen did not, contrary to aspen's prolific root suckering in upland sites. This asexual reproduction may lead to skewed sex ratios. Gom and Rood (1999) measured clonal sprouting that was stimulated by physical disturbance that accounted for a female-biased sex ratio among trees. For *P. balsamifera*, Comtois et al. (1986) measured the presence of male trees at higher frequencies on extreme sites, and female trees on protected, nutrient-rich sites. For aspen, Grant and Mitton (1979) measured an increase in male trees relative to

female trees at higher elevations compared to lower elevations. They also recorded higher radial growth rates of female trees compared to male trees. The finding that female trees exceeded male trees in both vegetative and sexual expenditures countered theories that sexual reproduction is metabolically more expensive for males than for females (Grant and Mitton 1979).

*Processes controlling cottonwood establishment*

Because cottonwood seeds lack endosperm, they require bare, moist soils to obtain light and nutrients for growth (reviewed in Braatne et al. 1996). Fluvial processes, such as channel narrowing, channel meandering, and flood deposition, create the bare surfaces required for cottonwood establishment (Bradley and Smith, 1986, Scott et al. 1994, Scott et al. 1997). The resulting distribution of cottonwoods provides visual records of historic floods and channel migrations, a forest that is "a living record of the recent migration of the channel" (Everitt 1968). When river channels narrow or avulse, the channel abandons a portion of its bed, leaving a surface for vegetation establishment. Along narrowed channels, cottonwoods grow in variable spatial patterns at low elevations in the former channel bed (Scott et al. 1994). However, on rivers where the water table is near the surface, soils in low-elevation sites, such as in abandoned river channels, may be too saturated in the spring for cottonwoods to colonize (M. Harner, personal observations). These sites may favor establishment of fall-seeding, or more moisture tolerant plants, such as alder. Cottonwoods also establish along point bars formed from the deposition of river sediments. When channels meander within an alluvial flood plain, the water erodes concave banks and deposits sediments on convex banks, leading to

extension of the point-bar (Leopold 1994) and subsequent colonization by cottonwoods in arcuate bands of even-aged trees (Everitt 1968). Along confined river reaches, sediment deposition from high flows (recurrence interval of at least 7 years) followed by high precipitation, may permit cottonwood colonization (Stromberg et al. 1991). Cottonwoods on flood deposits often grow in linear stands above the elevation of the channel bed (Scott et al. 1994).

Cottonwood seedlings establish along moisture gradients, with trade-offs between water table access and protection from physical disturbances (Segelquist et al. 1993, Mahoney and Rood 1998). Soil moisture becomes available to cottonwoods from the water table and the capillary fringe. Mahoney and Rood (1998) developed a growth model known as the 'recruitment box' that defines stream stage patterns that enable successful establishment of cottonwood seedlings. According to the model, a combination of root growth (0.5-1 cm/day), stream decline (<2.5 cm/day), and flood recurrence (1 in 5 to 1 in 10 years) are required for recruitment. They found that roots grow 0.5-1 cm/day, or 60-100 cm the first year. Segelquist et al. (1993) measured increased root and shoot growth for seedlings with gradual water table declines (0.4 cm/day). Rood et al. (2000) compared water table declines of 0, 2, and 4 cm/day and found that for 2 cm/day treatments, root elongation doubled, but leaf area decreased compared to the 0 cm/day treatment. Seedlings subjected to 4 cm/day declines in water table elevations suffered from drought stress that resulted in leaf senescence and abscission (Rood et al. 2000). Although seedlings benefit from access to soil moisture, the sites conducive to gradual declines in water table often occur at low elevations where seedlings are subjected to inundation and ice scour (Mahoney and Rood 1998).

Therefore, seedlings that establish in protected microsites or at the dry end of the moisture gradient may have the highest probability of growing to maturity (Segelquist et al.1993).

Cottonwoods access water from the capillary fringe, a zone of moisture above the water table, and fine roots responsible for water uptake occur in this region (Mahoney and Rood 1998). Because seedling roots may not reach the water table until their third or fourth growing season, the seedlings rely on soil moisture from precipitation and capillary action during these early years (Cooper et al. 1999). The texture of the soil affects its water holding capacity and the extent of the capillary fringe. Coarser substrates have smaller capillary fringes (about 5 cm), and medium textured sands have a fringe around 70 cm (Mahoney and Rood 1991). Therefore, trees that grow in coarse substrates, such as gravel, have less access to water. For seedlings of *P. balsamifera* X *P. deltoides*, Mahoney and Rood (1992) found that declines in water table combined with coarse substrates lead to decreased transpiration, height, leaf number, leaf area, and plant health. Others have found that cottonwoods may locally adjust their root architecture to adapt to site-specific water table regimes (Scott et al. 2000). Busch and Smith (1995) found that at sites with variable hydrology (intermittent flow), cottonwoods had deeper, more dispersed roots. At stable hydrologic sites (gaining reaches), trees had a shallower distribution of roots. Cottonwoods exposed to drought may have increased control of stomates (Pezeshki and Hinckley 1982, Schulte et al. 1987) and may maintain low osmotic potentials (reviewed in Blake et al. 1996).

*Effects of stream regulation*

Alterations of river landscapes by humans interfere with the establishment and growth of cottonwoods and threaten the existence of cottonwood forests. Dams, diversions, development, cattle grazing, and plant invasions are particularly damaging to cottonwoods. The survival of cottonwoods depends on managing regulated rivers in ways that mimic natural flows (Mahoney and Rood 1998, Rood et al. 1998) and by protecting intact riparian zones.

In the mid-1980s, researchers began documenting a lack of regeneration and senescence of cottonwood stands downstream of dams (Bradley and Smith 1986 and Rood and Heinze-Milne 1989). Because cottonwood trees depend upon fluvial disturbances to scour competing vegetation and to deposit alluvium, floods are necessary for cottonwood recruitment (Sigafoos 1964, Bradley and Smith 1986, Rood and Mahoney 1995, Scott et al. 1997, Rood et al. 1998). Decreased discharges and altered river stages prevent cottonwood regeneration by reducing bank scouring and sediment deposition necessary for seedlings to establish and by dropping ground water levels faster than plant roots can grow (Rood and Mahoney 1990, Mahoney and Rood 1998). Comparing stands upstream and downstream of a dam on the Kootenay River in Montana, Polzin and Rood (2000) documented hydrologic, geomorphic, and vegetative changes that decreased success of cottonwood seedlings at the downstream sites. These included reduced channel movement, depletion of fine sediments, reduced wood, and upland vegetation encroachment on floodplain surfaces. On other rivers, disruptions to natural flows have led to increased growth of vegetation within river channels (Johnson 1994). However, river regulation and cottonwoods can coexist, but dam releases must match cottonwood

life histories. Rood and Mahoney (1990) suggested: 1) having occasional spring floods; 2) gradually reducing peak flows, rather than abruptly declining river stage; and 3) maintaining sufficient flows through the summer.

Changes to river flows also affect species utilization of cottonwoods. Andersen et al. (2000) found that a small mammal, *Microtus montanus*, reduced seedling and sapling survivorship more on a regulated river site (Green River) compared to a free-flowing river (Yampa River). They suggest that on the regulated river, *Microtus* populations increased from not being exposed to spring floods, as well as benefited from cover provided from increased understory that was promoted by regulated flow.

Furthermore, cottonwoods require access to ground water for establishment (Segelquist et al. 1993, Mahoney and Rood 1998, Cooper et al. 1999) and survival (Busch and Smith 1995, Scott et al. 1999). River diversions, channel incisions, and decreased water tables lead to unnatural drought conditions that are particularly damaging to seedlings and old cottonwoods. Scott et al. (1999) studied effects on mature cottonwood trees of water table drops as a result of in-channel sand mining in Colorado. For declines >1 m, cottonwood trees had increased leaf desiccation, branch die-back, and significant declines in live crown volume within three weeks, which contributed to increased probability of mortality the following year. Following a natural channel incision resulting from a flood, Scott et al. (2000) measured water table declines that exceeded 1.5 m. Where water tables dropped more than 1 m, they observed 58-93% mortality in cottonwood stands. Where water tables dropped greater than 1 m, they observed mortality in 7-13% of the trees. Tree ring increments also decreased following the decline of water table.

Rivers provide corridors and sources for exotic plant invasions (Stohlgren et al. 1998), and regulated flows augment colonization by some exotic species. As a result of inadequate scour and deposition by floods, cottonwood seedlings do not have sites ideal for recruitment (Braatne et al. 1996), and exotic species that do not require scoured and deposited sites colonize in place of cottonwoods. In the southwestern United States, salt cedar (*Tamarix ramosissima*) from southeast Asia, which is tolerant of salinity, competes with native cottonwood (Howe and Knopf 1991, Dixon and Johnson 1999). Plains cottonwood species are threatened by invasions of Russian Olive (*Elaeagnus angustifolia*), a Eurasian species planted for bank stabilization and wildlife habitat (Shafroth et al. 1995, Lesica and Miles 2001). In the northwest, maple species including silver and Norway maple invade riparian sites (M. Harner, personal observation). Competitive advantages of some exotics over cottonwoods include shade tolerance (Lesica and Miles 2001), delayed germination (Shafroth et al. 1995), and lack of herbivore use, such as by beavers (Lesica and Miles 2001). Changes in species compositions from cottonwoods to nonnative shrubs or trees affect both the structure and function of the ecosystem, such as by altering canopies, and thus nesting sites. Differences in leaf chemistry, rooting structures, and wood decomposition also alter ecosystem function.

*Cottonwoods as repositories of environmental information*

The distribution (Everitt 1968) and wood scars (Sigafoos 1964) of cottonwoods reflect the histories of disturbance surrounding the trees. By studying cottonwood tree rings, one can estimate the age of cottonwoods (Clark 1987), and thus approximate

"...the time of the cessation of absolute domination of the cottonwood by the river, the real 'birth' of the flood-plain forest" (Everitt 1968). Using cottonwood ring counts, Everitt mapped meander patterns through time and developed contour maps of the Little Missouri River. This provided a history of the channel locations on a flood plain beyond information available from field observations and photographs. The age distribution of cottonwoods also reveals alterations to community structure resulting from human activities. For example, Merigliano (1996) used cottonwood ages to compare cottonwood establishment before and after flow regulation on the Snake River. Stromberg and Patten (1996) used tree rings to relate radial growth of black cottonwood to annual stream flow.

The wood of cottonwoods also reflects histories of disturbance. Cottonwoods have diffuse-porous wood, which means that early-wood vessels are small, and latewood vessels are not visible to the unaided eye (Telewski et al. 1996). Cottonwoods produce juvenile, tension, sapwood, and heartwood. The reaction wood of tension wood allows cottonwoods to rebound after bending, such as by burial from sediment or impact from log debris (Everitt 1968). Circumferential growth occurs around trunk scars on cottonwood trees. By comparing the position of the scar relative to the age (ring) of the tree, physical disturbances, such as by ice, wood, and fire can be dated (Sigafoos 1964). The position of the damage on the trunk also indicates the magnitude of the damage. For example, on Nyack Flood Plain on the Middle Fork of the Flathead River, river sediments were ingrained in the wood of cottonwoods at the elevation of the river stage during the 1964 flood (C. Dalimata, personal communication). On the Yakima River in Washington, scars on the bark of the cottonwood trees show the elevation of river stages

during previous floods (M. Lorang, personal communication). Thus, cottonwoods show legacies of stream corridors through their distribution along former or current river channels and through the scars that reflect the disturbance histories of the landscape. Furthermore, the productivity of cottonwoods may be influenced by sub-surface hydrologic patterns associated with groundwater flow. Therefore, cottonwoods serve as repositories of histories of both above and below ground floodplain processes.

## Literature Cited


Abbe, T.M. and D.R. Montgomery. 1996. Large woody debris jams, channel hydraulics, and habitat formation in large rivers. Regulated River Research and Management 12: 201-221.

Andersen, D.C. and D.J. Cooper. 2000. Plant-herbivore-hydroperiod interactions: effects of native mammals on floodplain tree recruitment. Ecological Applications 10:1384-1399.

Andrade, G., K. Mihara, R. Linderman, and G. Bethlenfalvay. 1998. Soil aggregation status and rhizobacteria in the mycorrhizosphere. Plant and Soil 202:89-96.

Bessey, C.E. 1901. The annual shedding of cottonwood twigs. Science 12:650.

Blake, T.J., J. Sperry, T.J. Tschaplinski, and S.S. Wang. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. *In* Biology or *Populus* and its implications for management and conservation. Part II, Chapter 16. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. pp. 401-422.

Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. *In* Biology or *Populus* and its implications for management and conservation. Part I, Chapter 3. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. pp. 57-85.

Bradley, C.E. and D.G. Smith. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. Canadian Journal of Botany. 64:1433-1422.

Brayshaw, T.C. 1965. The status of the black cottonwood (*Populus trichocarpa* Torrey and Gray). Canadian Field-Naturalist 79:91-95.

Brundrett, M., G. Murase, and B. Kendrick. 1990. Comparative anatomy of roots and mycorrhizae of common Ontario trees. Canadian Journal of Botany 68:551-578.

Busch, D.E. and S.D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S.. Ecological Monographs. 65:347-370.

Caldwell, M.M. and J.H. Richards. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. Oecologia 79:1-5.

Carothers, S.W., R.R. Johnson, and S.W. Aitchison. 1974. Population structure and social organization of southwestern riparian birds. American Zoologist 14:97-108.

Clark, S. 1987. Potential for use of cottonwoods in dendrogeomorphology and paleohydrology. M.S. Thesis. The University of Arizona Department of Geosciences. 52 pages.

Comtois, P., J.P. Simon, S. Payett. 1986. Clonal constitution and sex ratio in northern populations of balsam poplar, *Populus balsamifera*. Holarctic Ecology 9:251-260.

Cooper, D.J., D.M. Merritt, D.C. Andersen, and R.A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the Upper Green River, USA. Regulated Rivers: Research and Management 15:419-440.

Cummins, K.W. 1974. Structure and function of stream ecosystems. BioScience 24:631-641.

Cummins, K.W., J.R. Sedell, F.J. Swanson, G.W. Minshall, S.G. Fisher, C.E. Cushing, and R.C. Petersen, and R.L. Vannote. 1983. Organic matter budgets for stream ecostystems. *In* Stream Ecology: Application and testing of general ecological theory. *Edited by* J.R. Barnes and G.W. Minshall. Plenum, New York, NY. pp. 299-353.

DeBell, D.S. 1990. *Populus trichocarpa* Torr. & Gray: black cottonwood. *In* Silvics of North America: hardwoods. Vol. 2. *Edited by* R.M. Burns and B.H. Honkala. U.S. Department of Agriculture, Agriculture Handbook. pp. 570-576.

De Freitas, P.L., R.W. Zobel, and V.A. Snyder. 1996. A method for studying the effects of soil aggregate size and density. Soil Society of America Journal 60:288-290.

Dixon, M.D. and W.C. Johnson. 1999. Riparian vegetation along the Middle Snake River, Idaho: Zonation, geographical trends, and historical changes. Great Basin Naturalist. 59:18-34.

Eckenwalder, J.E. 1996. Systematics and evolution of *Populus*. *In* Biology or *Populus* and its implications for management and conservation. Part I, Chapter 1. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. pp. 7-32.

Emerman, S.H. and T.E. Dawson. 1996. Hydraulic lift and its influence on the water content of the rhizosphere: an example from sugar maple, *Acer saccharum.* Oecologia 108:273-278.

Everitt, B.L. 1968. Use of the cottonwood in an investigation of the recent history of a floodplain. American Journal of Science 266:417-439.

Farmer, R.E., Jr. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. *In* Biology or *Populus* and its implications for management and conservation. Part I, Chapter 2. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. pp. 33-55.

Fetherston, K.L., R.J. Naiman, R.E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Journal of Geomorphology 13:133-144.

Finch, D.M. and L.R. Ruggiero. 1993. Wildlife and biological diversity in the Rocky Mountains and Northern Great Plains. Natural Areas Journal 13:191-203.

Galloway, G. and J. Worrall. 1979. Cladoptosis: a reproductive strategy in black cottonwood? Canadian Journal of Forest Research 9:122-125.

Gom, L.A. and S.B. Rood. 1999. Patterns of clonal occurrence in a mature cottonwood grove along the Oldman River, Alberta. Canadian Journal of Botany 77:1095-1105.

Grant, M.C. and J.B. Mitton. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. Evolution 33:914-918.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. BioScience 41:540-551.

Hansen, E.A. and R.E. Dickson, 1979. Water and mineral nutrient transfer between root systems of juvenile *Populus*. Forest Science 25:247-252.

Howe, W.H. and F.L. Knopf. 1991. On the imminent decline of Rio Grande cottonwoods in central New Mexico. Southwestern Naturalist 36:218-224.

Johnston, C.A. and R.J. Naiman. 1990. Browse selection by beaver: effects on riparian forest composition. Canadian Journal of Forest Research 20:1036-1043.

Johnson, W.C. 1994. Woodland expansion in the Platte River, Nebraska: patterns and causes. Ecological Monographs 64:45-84.

Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373-386.

Kollmann, J., M. Vieli, P.J. Edwards, K. Tockner, and J.V. Ward. 1999. Interactions between vegetation development and island formation in the alpine river Tagliamento. Applied Vegetation Science 2:25-36.

Krasny, M.E., K.A. Vogt, and J.C. Zasada. 1988a. Establishment of four *Salicaceae* species on river bars in interior Alaska. Holarctic Ecology 11:210-219.

Krasny, M.E., J.C. Zasada, and K.A. Vogt. 1988b. Adventitious rooting of four *Salicaceae* species in response to a flooding event. Canadian Journal of Botany 66:2597-2598.

Leopold, L.B. and M.G. Wolman. 1957. River channel patterns: Braided, meandering, and straight. U.S. Geological Survey Professional Paper 282-B. p. 39-85.

Leopold, L.B. 1994. A view of the river. Havard University Press, Campbridge, MA. 298 p.

Lesica, P. and S. Miles. 2001. Natural history and invasion of Russian olive along eastern Montana Rivers. Western North American Naturalist 61:1-10.

Mahoney, J.M. and S.B. Rood. 1991. A device for studying the influence of declining water table on poplar growth and survival. Tree Physiology 8:305-314.

Mahoney, J.M. and S.B. Rood. 1992. Response of a hybrid poplar to water table decline in different substrates. Forest Ecology and Management 54:141-156.

Mahoney, J.M. and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment--an integrative model. Wetlands 18:634-645.

Martinsen, G.D., E.M. Driebe, and T.G. Whitham. 1998. Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. Ecology 79:192-200.

McGinley, M.A., and T.A. Whitham. 1985. Central place foraging by beavers (*Castor canadensis*): test of foraging predictions and the impact of selective feeding on the growth form of cottonwoods (*Populus fremontii*). Oecologia 66:558-562.

Merigliano, M.F. 1996. Ecology and management of the South Fork Snake River cottonwood forest. Idaho BLM Technical Bulletin 96-9.

Pezeshki, R. and T.M. Hinckley. 1982. The stomatal response of red alder and black cottonwood to changing water status. Canadian Journal of Forest Research 12:761-771.

Polzin, M.L. and S.B. Rood 2000. Effects of damming and flow stabilization on riparian processes and black cottonwoods along the Kootenay River. Rivers 7:221-232.

Pregitzer, K.S. and A.L. Friend. 1996. The structure and function of *Populus* root systems. *In* Biology or *Populus* and its implications for management and conservation. Part II, Chapter 14. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. pp. 331-354.

Richards, J.H. and M.M. Caldwell. 1987. Hydraulic lift: Substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73:486-489.

Rillig, M.C., S.F. Wright, M.F. Allen, and C.B. Field. 1999. Rise in carbon dioxide changes soil structure. Nature 400:628.

Rood, S.B. and S. Heinze-Milne. 1989. Abrupt downstream forest decline following river damming in southern Alberta. Canadian Journal of Botany 67:1744-1749.

Rood, S.B. and J.M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in Western prairies: Probable cause and prospects for mitigation. Environmental Management 14:451-464.

Rood, S.B. and J.M. Mahoney. 1995. River damming and riparian cottonwoods along the Marias River, Mt. Rivers 5:195-207.

Rood, S.B., A.B. Kalischuk, and J.M. Mahoney. 1998. Initial cottonwood seedling recruitment following the flood of the century of the Oldman River, Alberta, Canada. Wetlands 18:557-570.

Rood, S.B., K. Zanewich, C. Stefura, and J.M. Mahoney. 2000. Influence of water table decline on growth allocation and endogenous gibberellins in black cottonwood. Tree Physiology 20:831-836.

Schulte, P.J., T.M. Hinckley, and R.F. Stettler. 1987. Stomatal response of *Populus* to leaf water potential. Canadian Journal of Botany 65:255-260.

Schultz, R.C., J. G. Isebrands, and P.P. Kormanik. 1983. Mycorrhizae of poplars. *In* Intensive plantation culture: 12 years of research. *Edited by* E.A. Hansen. General Technical Report NC-91. U.S. Department of Agriculture Forest Service, St. Paul, MN. pp. 17-28.

Scott, M.L., J.M. Friedman, and G.T. Auble. 1994. Fluvial process and the establishment of bottomland trees. Geomorphology 14:327-339.

Scott, M.L., G.T. Auble, and J.M. Friedman. 1997. Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecological Applications 7:677-690.

Scott, M.L., P.B. Shafroth, and G.T. Auble. 1999. Responses of riparian cottonwoods to alluvial water table declines. Environmental Management 23:347-358.

Scott, M.L., G.C. Lines, and G.T. Auble. 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. Journal of Arid Environments 44:399-414.

Segelquist, C.A., M.L. Scott, and G.T. Auble. 1993. Establishment of Populus deltoides under simulated alluvial groundwater declines. American Midland Naturalist. 130:274-285.

Shafroth, P.B., G.T. Auble, and M.L. Scott. 1995. Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic Russian-olive (*Elaeagnus angustifolia* L.). Conservation Biology 9:1169-1175.

Sigafoos, R.S. 1964. Botanical evidence of floods and flood-plain deposition. Geological Survey Professional Paper 485-A. 35 pages.

Stanford, J.A. and J.V. Ward. 1986.The Colorado River system. Pages 353-374. *in* B.R. Davies and K.F. Walker (Editors). The Ecology of River Systems. Dr. W. Junk Publishers, Dordrecht, The Netherlands.

Stohlgren, T.J., K.A. Bull, O. Yuka, C.A. Villa, and M. Lee. 1998. Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecology 138:113-125.
Stromberg, J.C., D.T. Patten, and Richter, B.D. 1991. Flood flows and dynamics of Sonoran riparian forests. Rivers 2:221-235.

Stromberg, J.C. and D.T. Patten. 1991. Instream flow requirements for cottonwoods at Biship Creek, Inyo County, California. Rivers 2:1-11.

Stromberg, J.C., B.D. Richter, D.T. Patten, and L.G. Wolden. 1993. Response of a Sonoran riparian forest to a 10-year return flood. Great Basin Naturalist 53:118-130.

Stromberg, J.C. and D.T. Patten. 1996. Instream flow and cottonwood growth in the Eastern Sierra Nevada of California, USA. Regulated Rivers: Research and Management 12:1-12.

Stromberg, J.C., R. Tiller, and B. Richter. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. Ecological Applications 6:113-131.

Telewski, F.W., Aloni, R. and Sauter, J.J. 1996. Physiology of secondary tissues of *Populus*. *In* Biology of *Populus* and its implications for management and conservation. Part II, Chapter 13. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, Ontario. pp. 301-329.

Tisdall, J.M., S.E. Smith, and P. Rengasamay. 1997. Aggregation of soil by fungal hyphae. Australian Journal of Soil Research 35:55-60.

Triska, F.J., V.C. Kennedy, R.J. Avanzino, G.W. Zellweger, and K.E. Bencala. 1989. Retention and transport of nutrients in a third-order stream: channel processes. Ecology 70:1877-1892.

Vozzo, J.A. and E. Hacskaylo. 1974. Endo- and ectomycorrhizal associations in five *Populus* species. Bulletin of the Torrey Botanical Club 101:182-186.

Waltz, A.M. and Whitham, T.G. 1997. Plant development affects arthropod communities: opposing impacts on species removal. Ecology 78:2133-2144.

Whitham, T.G., G.D. Martinsen, K.D. Floate, H.S. Dungey, B.M. Potts, and P. Keim. 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. Ecology: 80:416-428.

Wright, S.F. and A. Upadhyaya. 1996. Extraction of an abundant and usual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. Soil Science 161:575-586.

Wright, S.R. and A. Upadhyaya. 1998. A survey of soils for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. Plant Soil 198:97-107.

Zasada, J.C. and H.M. Phipps. 1990. *Populus balsamifera* L.: balsam poplar *In* Silvics of North America: hardwoods. Vol. 2. *Edited by* R.M. Burns and B.H. Honkala. U.S. Department of Agriculture, Agriculture Handbook. pp. 518-529.

# Chapter 2

## Growth and Distribution of *Populus trichocarpa* on an Alluvial Flood Plain

### Introduction

Interstitial flow within floodplain aquifers influences physical, chemical, and biological properties of alluvial rivers (Stanford and Ward 1993, Boulton 1998, Jones 2000). The vertical exchange of surface water and ground water in hyporheic zones produces temporal and spatial variation in water availability, nutrient concentrations, and water temperatures. On large alluvial rivers, these gradients have been shown to influence microbial assemblages (Ellis et al. 1998), fish spawning (Cavallo 1997), benthic assemblages (Pepin and Hauer 2001), and algal biomass (Bansak 1998), among many other biophysical attributes (Naiman et al. 2000). However, few studies have considered the response of riparian vegetation to vertical and lateral gradients of interstitial water flux. Hyporheic zones, defined by penetration of river water and river organisms into the bed sediments (Stanford and Gaufin 1974), that extend laterally into the riparian forest may influence vegetation by increasing the availability of water and nutrients.

Cottonwood trees are major biological and physical components of flood plains throughout the Northern Hemisphere. They create wildlife habitat (Carothers et al. 1974, Finch and Ruggiero 1993, Saab 1999, Anderson et al. 2000) and forage (Johnston and Naiman 1990, Anderson and Cooper 2000), provide nutrients to streams and soil from leaves (Wallace et al. 1997), affect geomorphology by depositing wood boles to streams (Fetherston et al. 1995, Abbe and Montgomery 1996, Bilby and Bisson 1998), influence the assemblages of herbivores (Whitham et al. 1999), and hold importance for human

recreational and cultural values. However, riparian cottonwood forests are senescing and declining along rivers as a result of altered river hydrology (Rood and Heinze-Milne 1989, Rood and Mahoney 1990, Merigliano 1996, Polzin and Rood 2000) and cattle grazing (Crouch 1979, Armour et al. 1991, Fleischner 1994). Restoration and protection of cottonwoods depend on understanding the tree's life history requirements in relation to natural river processes (Braatne et al. 1996).

Variation in river and floodplain hydrology within reaches (<10 km) and associated upwelling zones may influence cottonwood productivity and distribution by delivering water and dissolved forms of nitrogen and phosphorus to riparian vegetation. Ground water may contain substantially more N and P than surface water, due to hypogean metabolism of organic matter (Dahm et al. 1998). Algal production is often high in areas where ground water upwells to the surface (Grimm and Fisher 1984, Valett et al. 1994, Valett et al. 1997). Water enriched by nitrogen and phosphorus released from interstitial food webs (Ellis et al. 1998) may become available to riparian plants through paleochannels (buried former river channels) or other subsurface flow paths (Triska et al. 1993). How natural nutrient loading in groundwater may affect riparian tree productivity has not been studied, although uptake of nutrients by streamside vegetation (buffer zones) is thought to be a way of controlling stream eutrophication in areas where groundwater flows from uplands to the river (Lowrance et al. 1984, Peterjohn and Correll 1984).

In a long-term study on the Flathead River, Stanford and Ward (1988) and Stanford et al. (2001) measured penetration of river water into the alluvial aquifer. As the water flowed through the alluvium, transformations occurred that resulted in increased nitrate, phosphorus, and oxygen in hyporheic waters relative to the river channel (Stanford et al. 1994, Ellis et al. 1998). Bursts of algal productivity were

observed where the hyporheic water discharged into surface flows (Bansak 1998). Well measurements and ground-penetrating radar studies clearly showed zones of high hydraulic conductivity (Poole et al. 1997), causing preferential routing of ground water at high rates that approached 10 cm/s (Stanford et al. 1994). These preferential flow paths varied in length, from a few meters to several kilometers, and were apparently formed by natural backfilling of abandoned river channels (Stanford and Ward 1988, Poole et al. 2001) mediated by the interaction of large wood and sediment recruitment (Naiman et al. 2000). The subsequent filling of abandoned channels by sediments created zones of preferential groundwater flow within alluvial aquifers (Huggenberger et al. 1998) that strongly influenced floodplain hydrology (Poole 2000). As a result of the dynamic hydrology and the influence of flow variability on soil and aquifer nutrient cycling processes, the water that cottonwood roots access on flood plains, such as Nyack, likely is not homogenous in terms of availability or nutrient supply.

Vegetation also may contribute nutrients to ground waters via exudates from the rhizosphere. Indeed, Bechtold (2000) and Naiman et al. (2000) suggested that organic matter supply in ground waters could be derived primarily from litter decomposition in the floodplain soils rather than from entrainment of organic matter from the river. In 1996, researchers discovered a protein on hyphae of arbuscular mycorrhizal fungi and isolated the protein, glomalin, from soils (Wright and Upadhyaya 1996). Root fungi from the order *Glomales* produce the glycoprotein named glomalin. The accumulation of carbon (20-30% of structure), as well as nitrogen, in the protein creates nutrient stores in soils (Jastrow et al. 1996, Rillig et al. 1999) that may leach into ground water. The protein has been found to enhance soil stability by contributing to the binding of soil particles (Wright and Upadhyaya 1998, Wright et al. 1999). These soil structures affect

plant productivity by providing habitat for microorganisms that mobilize nitrogen and phosphorous (De Freitas et al. 1996, Andrade et al. 1998). The protein is also downwardly mobile and transferred in water (M. Rillig, personal communication). However, protein distribution and transport have not been documented in soils or in relation to groundwater ecology of river flood plains. Exudates from the rhizosphere, such as fungal glycoproteins, may have far-reaching influences on riparian ecosystems by increasing nutrient storage in soils, as well as leaching nutrients to interstitial food webs.

Interstitial flow and down- and upwelling at large ($km^2$) spatial scales seem to affect many aspects of floodplain ecology (Stanford and Ward 1988, 1993, Stanford et al. 1994, Cavallo 1997, Ellis et al. 1998, Bansak 1998, Pepin and Hauer 2001). Since cottonwoods greatly influence, or appear to play a direct role in these processes, I examined how the cottonwood forests on an expansive flood plain of the Middle Fork of the Flathead River responded to interstitial flow and the associated biophysical processes. The objective was to describe growth and distribution of cottonwoods in losing and gaining reaches of a flood plain in relation to a 60-year-record of channel scour and avulsion that created areas where cottonwood seedlings established.

**Study Site**

Nyack Flood Plain is located near West Glacier, Montana, on the Middle Fork of the Flathead River, a 5th order unregulated river (Fig. 1). Nyack Flood Plain occurs within a glacier-carved valley, through which the Middle Fork drops an average of 1.5 m/km. Most of the Middle Fork drainage is pristine, as its headwaters lie in the Great Bear Wilderness of the Flathead National Forest, and the valley segment flows along the

south boundary of Glacier National Park. However, construction and maintenance of a railroad and highway have altered small areas of flood plain.

Nyack Flood Plain is approximately 8 km long and 3 km wide and is constricted on the up- and downstream ends by bedrock. Between these knick points, the river avulses across a flood plain. A United States Geological Survey gauging station is located 19 km downstream of Nyack at West Glacier, Montana (www.montana.usgs.gov Station #12358500). Flood dates and peak discharges were available from 1939-2000. The Middle Fork has a hydrograph dominated by snowmelt and exceeds the National Weather Service flood stage of 305 cm about once a decade. The daily average discharge on Nyack is 82 $m^3/s$, peak annual discharge averages 541 $m^3/s$, and base flow averages 17 $m^3/s$. The largest flood on record occurred in 1964 and reached an estimated discharge of 3,962 $m^3/s$.

Average annual total precipitation was 75 cm from 1950-2000 based upon data from the Western Regional Climate Center (www.wrcc.dri.edu). Forest vegetation along the river includes black cottonwood (*Populus trichocarpa*), alder (*Alnus spp.*), and willow (*Salix spp.*). Mature riparian forest consists of Engelmann spruce (*Picea engelmannii*), Douglas-fir (*Pseudotsuga menziesii*), and subalpine fir (*Abies lasiocarpa*), which have grown under the cottonwood overstory (Wondzell 1992, Mouw et al. 2001). Old growth cottonwood trees reaching >1.5 m (DBH) are present in some stands.

Stanford et al. (2001) quantified the water mass balance of the flood plain by measuring discharge over a two-year period in all inflowing sources to the flood plain and in the river at the downstream knick point. Losing and gaining reaches were determined by spatial analyses of discharge in the main channel on 9 occasions

representing the range of flows from base to peak. This analysis was corroborated by quantifying the vertical hydraulic gradient with a piezometer net at or near the synoptic discharge sites. This work established that at the upstream end of the flood plain, the river losses 20-30% of its surface flow into the alluvial aquifer. This water moves through the alluvial aquifer and returns to the surface, creating spring brooks, ponds, wetlands, as well as contributing flow to the channel. Strong upwelling occurs at the lower flood plain, where 16% of the river flow comes from influent ground water. The reach distribution of downwelling and upwelling further was supported by spatial analysis of persistent habitats created by upwelling groundwater (D. Whited, J. Stanford and J. Kimball, Flathead Lake Biological Station. unpubl. data) at base river flows. Hence, two discrete reaches, one losing and one gaining, were available for analysis of cottonwood growth (Fig. 1).

## Methods

### *Overview*

Factors that influence the growth and distribution of cottonwoods were studied on an alluvial flood plain. The first objective was to compare the growth of cottonwood trees between a losing and gaining reach of Nyack Flood Plain and to examine the growth of cottonwoods in relation to variables that are influenced by channel scour and avulsion. The second objective was to describe the distribution of cottonwood trees in relation to peak river flows, flood scour, and channel abandonment during the period of record from 1945-2000. To describe the growth and distribution of cottonwood trees in reaches of contrasting hydrology on Nyack Flood Plain, 16 plots in a losing reach were compared to 16 plots in a gaining reach. The following variables were measured: rate of radial tree

growth, change in water table elevation over one growing season, plot elevation above river at base flow, depth of fine sediments, concentration of soil protein, soil stability, cottonwood stem density, plot age, and plot position relative to historic river channels.

*Plot selection*

A total of 32 circular plots were sampled: 16 plots were in the losing reach and 16 plots were in the gaining reach (Figs. 2 and 3). These reaches had contrasting hydrology, but were otherwise similar in vegetation composition, slope aspect, and land use (these areas were not influenced by cattle grazing or logging). A plot size of 200 $m^2$ was chosen because elevation, and therefore depth to water table, were relatively homogenous within this area. Larger areas often intersected wood jams, overflow channels, or depressions, which may have influenced trees by altering the accumulation of sediment and the availability of water. If fewer than 12 cottonwood trees within the 200 $m^2$ area, the plot size was increased to include 12 trees. To assure that an equal distribution of cottonwood ages were sampled, cottonwood stands were stratified *a priori* into size classes: seedling (trees < 5 years), sapling (DBH < 5 cm), pole (DBH = 5-20 cm), mature (DBH > 20 cm), and old growth (DBH > 20 cm *and* conifers in canopy). This was accomplished by identifying each type of stand on aerial photographs and in field surveys. The cottonwood stands on the photos were divided into polygons representing cohorts (approximately 20 cohorts in each reach), and plot locations were randomly selected for 10 of the plots. Other plots were sampled within established vegetation transects (Mouw et al. 2001) and near piezometers. Within reaches, approximately 80% of the total cottonwood cohorts within the currently active floodplain (i.e. scoured by flood in 1964) were sampled. Old growth stands were not included in the analysis

because the trees were too large to accurately determine age and growth by coring (see below), and the river recently has not avulsed through these stands. Regenerating stands less than 5 years old also were not included because small trees were not readily discernable on aerial photos.

### *Part 1: Factors that influence growth*

#### *Determination of growth rates of cottonwoods*

Radial growth rates of cottonwoods were compared between the losing and gaining reaches. Growth rates were determined in two ways. First, growth was estimated as a relationship between tree diameter and tree age. Second, the last ten years of growth were measured for each tree. As another estimate of cottonwood productivity, normalized vegetation index (NDVI) levels were compared on aerial photographs.

To determine tree age and measure growth rings, an increment borer (12 mm X 46 cm) was used to extract cores at 30 cm above the ground. During a pilot study, it was determined that a minimum of 12 trees was required to minimize standard error. Sampling more than 15 trees did not significantly increase the confidence of the mean age estimate. Therefore, in plots where increment cores were taken to determine tree age, 12-20 trees were randomly selected for core extraction. In plots with trees too small to core, trees were cut at 30 cm above ground. In these plots, fewer trees were sampled (7-10) because rings could be precisely counted on the cross sections. Obvious stump sprouts and root suckers were not aged. Tree heights were measured with a clinometer. Tree diameters at breast height were determined by measuring tree circumference with a calibrated tape. Cores were stored in wooden racks while in the field to protect the cores and to keep the wood from bending as it dried. After the cores air-dried for

approximately 5 days, they were mounted on grooved plywood boards, secured with wood glue, and sanded. A belt sander with 80 and 100 grit sand paper was used. Some cores required finer sanding by hand. For these, 600 grit sand paper was used.

To calculate growth rates over the entire life of the tree, DBH was related to tree age using a regression model (Fig. 4). To determine age, tree rings were counted with the aid of a hand lens or microscope. To create homogeneous variance, DBH was log transformed. A regression of DBH and age was calculated to determine residuals (Fig. 4). Studentized residuals were used as an index of growth rate for each tree. This regression removed the effect of age on growth (i.e. young trees tended to grow faster). However, variation in stand density during the early life of the tree, which may have affected growth, could not be determined.

To calculate growth rate for the last ten years, which accounts for present stand density, basal area growth was calculated for each tree. To measure basal area growth for the last ten years, the total length of the last ten ring increments were measured with calipers. The area of ten year's growth was then compared with the total tree area:

$$\text{Basal area growth per tree} = \text{radial growth per 10 years} * \pi * (D_0\text{-}D_1/2)$$

$D_1$ = Diameter of inner circle (total-10years)

$D_0$ = Diameter of outer circle, excluding bark.

Additionally, to estimate overall plot productivity, BA growth for the last ten years was expanded to include stem density and the average BA growth was calculated for each plot.

$$\text{Basal area growth per plot} = \text{average BA growth/tree} * \#\ \text{stems/area}$$

As another estimate of the cottonwood productivity within reaches, normalized difference vegetation index (NDVI) levels were compared between plots. NDVI was

measured as the relationship between NIR-Red/NIR+Red obtained from the advanced very high resolution (AVHR) image of the flood plain photographed in 1999. Growth rates of cottonwood trees were regressed against calculated NDVI values to determine if productivity could be estimated through remotely sensed data and to determine if the remotely sensed data would corroborate reach differences determined by plot measures.

*Measurements of factors influential to growth*

Plot variables that might explain variation in cottonwood growth between reaches and between plots were measured. The measured variables included: change in water table elevation over one growing season, plot elevation above river at base flow, depth of fine sediments, concentration of soil protein, and soil stability, and cottonwood stem density.

To quantify variation in hydrology between the losing and gaining reaches, surface water and ground water elevations were measured by surveying river stage and monitoring water table dynamics with piezometers. To measure water table elevations away from the active channel, piezometers were installed on the flood plain. Six piezometers were placed in the losing reach of the flood plain and five were placed in the gaining reach. Eight of the piezometers were located in sampled plots. From the piezometers, water table elevations were measured relative to river discharge. Water levels in the piezometers were measured weekly from April-August 2000, when river reached base flow, or until the piezometers went dry. A data logger located at the upstream end of the flood plain continuously recorded river stage. Temporal patterns relating river and the groundwater elevations for each piezometer were developed to examine groundwater hydrology within plots.

To measure plot elevations above base flow (11.3 $m^3/s$ on September 22 and 23, 2000), a laser theodolite was used to survey the flood plain. X and Y coordinates of plot centers were also measured, which permitted precise mapping of stand locations. Triangulation of survey shots required using a back sight relative to a known coordinate. A GPS was used to determine X,Y for the start of the survey. Triangulation came from the GPS point and a back sight to the fire lookout tower on Lone Man Mountain (UTM Zone 12, datum NAD 83, Northing: 295438.416, Easting: 5374147.75).

Depth to coarse material (the amount of fine sediments) was measured because the texture of the soil likely affects the height of the capillary fringe. Increased soil water would be expected in areas with finer textured soils. To measure soil characteristics, a soil pit was dug in the center of each plot. Depth to coarse material (large gravel or cobble) and the depth of each soil layer were recorded. For each layer, soil textures were described in the field by hand texturing.

Soil proteins were measured in the plots to determine if proteins occurred in flood plain soils. Soil samples from each horizon were collected from pits. The A horizons for each plot were analyzed using the Bradford assay (Wright and Upadhyaya (1996). To see if the aggregate stability of floodplain soils differed across the flood plain or in stands of different ages, soil aggregate stability was measured after the method of Kemper and Rosenau (1986). Water stable aggregates were expressed as a percentage of the total weight of aggregates subjected to sieving.

Stem density was measured to determine if growth per tree was influenced by proximity of other cottonwood trees. Cottonwood densities were measured by counting the number of stems within the area of each plot. Total basal area within a plot was calculated using measurements of tree diameters of all stems in a plot.

*Statistical analysis*

Each plot was considered the sample unit because trees growing within a plot likely were not independent of each other. To determine if growth differed more at certain age classes, the sample was stratified by age into three age classes: sapling, pole, and mature. For the sampled plots, sapling stands (n = 11) ranged in age from 7-15 years, pole stands (n = 10) from 20-35 years, and mature stands (n= 11) 36-67 years. These classes were natural breaks in the sample.

Analysis of variance (ANOVA) was used to compare growth rates of plots within the losing and gaining reaches and between the reaches. Three measurements of growth rate were compared: growth over the entire life of the tree, basal area growth per tree (1990-2000), and basal area growth per plot (1990-2000). Fixed factors were floodplain position (losing and gaining reaches) and stand type; random factors were plots. All statistics were conducted using SPSS.

Site variables were related to floodplain reach and plot type and between floodplain position within plot types using ANOVA and Tukey's post-hoc comparisons. Statistical significance was set at the five-percent level of probability ($p \leq 0.05$). Independent variables were tested for co-linearity; co-linear variables were not included in models. Analysis of covariance was used to describe the influence of site variables on growth rates. Fixed factors were floodplain position (losing and gaining reaches), and covariates included: depth to gravel, stand density, plot elevation above river base flow, concentration of protein in soil. Stem density was a factor in total growth and BA growth per tree analyses, but not for BA growth per plot analysis (density was accounted for in the calculation of independent variable). Additionally, forward-stepping multiple linear

regression was used to examine the relationships between site variables and growth rate indices (over the entire life of the tree) within age classes.

### *Part 2: Factors that influence distribution*

#### *Cottonwood establishment relative to peak river flows*

To determine if peak river discharges influenced establishment of cottonwood trees, tree establishment was correlated to river discharge by comparing the frequency of trees establishment each year (for all trees n = 402) to annual discharge. To estimate the actual number of trees established during a given discharge, tree mortality was estimated. This was accomplished by calculating the number of trees that died each year based on density measurements compared to stand ages. The mortality percentile was used to estimate the number of trees established in a specific year. The life table was calculated from 1960-1996, as regeneration estimates prior to that time were poor based on a small sample. The frequency of tree establishment was then correlated to the peak discharge. Because peaks in tree establishment occurred in average flow years, tree establishment was also correlated to total June precipitation and June temperature to determine if rain or temperature contributed to establishment.

#### *Cottonwood establishment in relation to flooding and channel avulsions*

To examine spatial distribution of plots and differences between plots, plot measurements were overlaid on a rectified photo series. Aerial photos of Nyack Flood Plain from 1945, 1966, 1981, and 1992 were scanned, georectified, and linked to a base map image from 1999. For each photo series, the river channel and mature vegetation patches were digitized in Arc/INFO. Plot locations were identified on each map using

the X,Y locations measured during the topographic surveying and were labeled on historical photos in Arc/INFO (Figs. 2 and 3). Areas scoured by floods and historic channel locations were visible on the photos. Therefore, it was possible to compare plot variables such as growth rate and stand age to channel change and flood scour over time.

## Results

### *Part 1: Factors that influence growth*

#### *Growth rates of cottonwoods*

Average tree growth compared over the entire life of the tree differed between the gaining and losing reaches (p=0.072), and trees in the gaining reach had higher radial growth (Fig. 5). Based on mean growth rate indices for each region, trees in the losing reach grew an average of 0.045 units *less* than the expected tree growth (calculated from Fig. 5). Trees in the gaining reach grew an average of 0.0843 units *faster* than the expected growth. Hence, an average 30 year-old tree on the flood plain had a DBH of 126 mm (calculated from Fig. 4): [BA = anti-log(2.1)]). From Fig. 5, an average 30 year-old tree in the losing reach had a smaller DBH of 114 mm [DBH = anti-log(2.1-0.045)]. An average 30 year-old tree in gaining reach had a larger DBH of 153 mm [DBH = anti-log(2.1+0.0843)]. This represented a 35% increase in diameter for trees growing in the gaining reach compared to trees growing in the losing reach. Similarly, a 10 year-old tree in the gaining reach would be expected to have a DBH 6.23 mm larger than in the losing reach. A 50 year-old tree in the gaining reach would have a DBH 93 mm greater than a tree of the same age in the losing reach.

Using plots as the sample unit, no significant differences in growth rates between age classes or between reaches within age classes were found (Fig. 6). However, the

trend of higher mean growth in gaining versus losing reaches observed for all trees taken together was evident. Plots were considered as the sample unit because of trees within a plot being dependent on each other. However, all tree data were used in the regression to determine growth residual (Fig. 4) to strengthen the relationship. This may violate assumptions of independence within a plot. However, when age/growth relationships were considered on a plot level, the variation was too great within a plot to determine a relationship from which to calculate a growth coefficient on a plot basis. If trees were considered as the sample unit for all analyses (though this was not the sample design), there was a significant difference in growth between the two reaches (mean growth index in losing reach = -0.058, in gaining reach = 0.0619). Growth rate between age classes also differed, with pole stands having a significantly ($p < 0.0001$) lower growth rate than both sapling and mature stands. Within age classes, growth was significantly different between reaches for mature stands ($p=0.001$) and pole stands showed a strong trend towards growth differences ($p=0.059$, Fig. 6).

Average basal area (BA) growth per tree and per plot (for 1990-2000), did not significantly differ between the losing and gaining reaches (Table 1). Average BA growth per tree was greater in the gaining reach compared to the losing reach. However, total BA growth per plot was slightly higher in the losing reach compared to the gaining reach (Table 1).

Another estimate of productivity, normalized difference vegetation index (NDVI) levels from cottonwoods, varied between reaches. In the losing reach, average NDVI levels were 50.6, compared to 76.4 in the gaining reach, but the means were not significantly different. However, variation in remotely sensed cottonwood productivity

(from NDVI signal) showed a positive relationship ($p=0.047$, $r^2 = 0.223$) to measured cottonwood growth rates.

*Factors influential to growth*

Measurements of water table elevations in the upper and lower reaches supported the pattern of regional downwelling and upwelling on Nyack Flood Plain. Elevation of the water table and river stage fluctuated together throughout the season (Fig. 7). However, cottonwoods growing in the losing and gaining reaches experienced different ground water stage declines throughout the summer. Over the growing season, water table decline differed between the losing and gaining reaches (Fig. 8). On average, the water table in the losing reach declined 80 cm more than in the gaining reach. Where ground waters declined the most over the growing season, cottonwood trees grew the least (Fig. 9).

Plot elevations (relative to elevation of the base flow in the channel) did not differ between the losing and gaining reaches, either within age classes or among plots. However, pole stands occurred, on average, at slightly higher elevations (20 cm) than mature stands. Sapling stands (7-15 years old) occurred 1.6 m (+/- 0.48 SD) above base flow. Pole stands (20-35 years old) occupied sites 2.2 m (+/- 0.58 SD) above base flow. Mature stands (35-70 years) stood 2.0 m (+/- 0.41 SD) above base flow. The oldest, but slightly lower elevation, stands (plots 3, 22, and 24, Fig. 2) occurred just downstream of the upper floodplain knick point. The lower elevation of the oldest stands may have resulted from scour during the 1964 flood that did not remove the large and well-rooted trees.

Fine sediments (i.e. depth to gravel or coarse material) were 29 cm thicker (measured from the surface) in the gaining reach (Fig. 10). Fine material was significantly deeper in mature stands compared to sapling ($p=0.005$) and to pole ($p=0.004$) stands. Between the losing and gaining reaches, depth to gravel did not significantly differ within age classes. However, within mature stands, there was a strong trend for plots in the gaining reach to have deeper layers of fine sediments. There was no correlation between the depth to coarse material and plot elevation.

The concentration of soil protein significantly ($p=0.045$) differed between the losing and gaining reaches (Fig. 11). On average, plots in the losing reach had 2.66 mg of protein per 1 gram of soil, and plots in the gaining reach had 4.49 mg/g. Protein concentration positively correlated with soil aggregate stability ($p < 0.0001$, $r^2 = 0.523$), plot age ($p=0.001$, $r^2 = 0.324$), depth to gravel ($p=0.032$, $r^2 = 0.144$), and soil fineness ($p=0.041$, $r^2 = 0.132$) and negatively correlated with stand density ($p<0.0001$, $r^2 = -0.489$). Within pole stands, there was a significant difference ($p=0.001$) between soil protein concentrations between the losing and gaining reaches (Fig. 11).

Exponential decline of tree density with plot age was observed (Fig. 12). Young cottonwood stands were very dense (>10,000 stems/ha), and thinned rapidly between 10 and 20 years. Stem exclusion ceased around 30 years, and densities in older stands were relatively constant and low (<1,300 stems/ha). Significant differences between cottonwood densities between the losing and gaining reaches, either within age classes, or across all stand types were not detected. However, in sapling stands, there was trend towards less dense stands in the gaining reach (mean = 11,933 stems/ha) compared to the losing reach (mean = 17,440 stems/ha). One plot appeared to be an outlier (Plot 21, see Fig 3 for plot location). The plot occurred in the gaining reach and exhibited the fastest

growth on the flood plain, growth rate index = 0.506 (measured over entire life of the tree). Plot 21 contained only cottonwood and willow, and willow root suckers extended from the stand toward the river. As plot age increased, there was an increase in total cottonwood basal area within plots. Basal area significantly differed between all age classes. Within age classes, there was a significant difference in total basal area within mature stands, where plots in the losing reach had higher total basal area than plots in the gaining reach. Although trees were smaller on average in the losing reach, there were more small trees in that reach and fewer larger trees in the gaining reach. The total basal area of the small trees exceeded that of the larger trees in the gaining reach.

To summarize, the results from measurements of variables potentially influential to cottonwood growth are as follows: When growth rate was measured over the entire life of the tree, cottonwoods grew faster in the in the gaining reach. In the gaining reach, the water table declined less over the growing season compared to the losing reach. Plot elevations above base flow ranged from 1.5-2.2 m. There was an increased accumulation of fine sediments in the gaining reach, and oldest stands had the greatest accumulation of fine sediments. Soil protein concentrations were significantly greater in the gaining reach and correlated with soil aggregate stability. Stem density declined with plot age, but plot densities did not differ between reaches.

*Analyses of variance*

Because water table measurements were only available for eight plots, statistical analyses focused on explaining variation in growth relative to other variables. Analysis of covariance for the three growth analyses are presented in Table 2. Significant differences in growth between the losing and gaining reaches were predicted for growth

measured over the entire life of the tree and for BA growth per tree. BA growth per plot did not differ between reaches.

Compared across the gaining and losing reaches, different site variables influenced cottonwood growth rates over the entire life of the tree depending on tree age based on multiple linear regression analysis. For all plots with water table measurements (n=8), plot elevation above base flow (p=0.002) and depth to water table (p=0.004) predicted tree growth ($r^2$=0.96). For all plots (no water table data included), depth to gravel (p=0.010) predicted tree growth. Within sapling stands, soil protein (p=0.001) and plot elevation above base flow (p=0.044) predicted tree growth ($r^2$= 0.801). Within pole stands, stand density (p=0.017) predicted tree growth ($r^2$ = 0.530). No linear models predicted tree growth in mature stands.

***Part 2: Factors that influence distribution***

*Tree establishment relative to peak river flows*

Peaks in cottonwood establishment were associated with highest flood flow on record: 1964, 1975, and 1990-91 (Fig. 13). Tree mortality estimates, calculated from density data (Fig. 12), suggested that the number of trees established increased as the flood peak increased. However, a pulse of cottonwoods that established between 1984-87 was not correlated with a large flood (maximum discharge was approximately 600 $m^3/s$ during this period). Establishment was not related to June temperature or precipitation, except for in wet years that were also high discharge years. The mean tree age for plots in the losing and gaining reaches combined was 28 years. The mean age of trees in the losing reach was 31 years (established in 1969), and 25 years (established in

1975) in the gaining reach. Within plot ages ranged up to 25 years in a few plots. However, the 95% confidence intervals of the mean age generally fell within a confidence interval of +/- 5 years of the mean. The oldest tree aged was 67 years (established in 1933) and the youngest was 7 years (established in 1993). Some trees in the old growth stands that were not included in the plots exceeded ages of 250 (established mid 1700s), based on coring from a pilot study.

*Cottonwood stand establishment in relation to river flooding and channel avulsions*

Cottonwood age-cohorts corresponded to flood scour and sediment deposition in the two reaches. In the losing reach, the greatest scouring (determined by analysis of the photographic series) occurred between 1945 and 1966, likely during the 1964 flood of record (Fig. 2). However, in the gaining reach, the greatest scouring occurred between 1966 and 1981, possibly during the 1975 flood (Fig. 3). The average tree age in the losing reach dated to 1969 and in the gaining reach to 1975, suggesting that different events stimulated cottonwood establishment within the two reaches.

Cottonwood stands sampled in the summer of 2000 predominately occurred near abandoned and refilled channels, and tree ages were related to channel ages (Figs. 14 and 15). Within sapling stands, 70% of the sampled plots occurred adjacent to the 1981 channel (75% in the losing reach, 66% in the gaining reach). Within pole stands, 83% of the total stands sampled were located adjacent to the 1945 river channel (87.5% in the losing and 75% in the gaining reach). Within mature stands, 60% of the total stands occurred adjacent to the 1945 river channel (75% in the losing and 50% in the gaining reach). Twenty five percent of the total plots occurred in the center of former river channels.

## Discussion

### *Factors influencing the growth of cottonwood trees*

Interstitial flow and the associated biophysical processes occurring on Nyack, a natural, dynamic flood plain, positively influenced the growth and distribution of cottonwood trees. Where groundwater flow was near the surface, such as through abandoned river channels (Poole 2000) and in the gaining reach, cottonwood trees established and grew faster (Fig. 5). The availability of ground water within the range of tree roots strongly correlated with tree growth (Fig. 9). Along with water availability, the nutrient content and temperature of effluent versus influent water may have affected growth, but these variables were not measured. Alternatively, site variables, such as soil texture, stand density, and plot elevation above base flow added variation to observed rates of growth. Because measurements of water table elevations were only available in one quarter of the sampled plots, variation associated with groundwater availability versus other variables could only be separated for eight plots. The strong correlation ($r^2$ = 0.96) between tree growth and change in water table elevation combined with plot elevation suggested that the availability of ground water was very influential to the growth of cottonwood trees.

Where water table elevations were lower at base flow, such as in the losing reach, cottonwood trees may have suffered from seasonal drought stress. Water stress may cause decreased productivity due to increased stomatal closure that reduces rates of photosynthesis. Drought stress was measured on the Bill Williams River in Arizona, where Busch and Smith (1995) compared *P. fremontii* in a gaining versus intermittent reach and found a trend of increased rates of stomatal conductance and transpiration and increased predawn and midday leaf water potential in the gaining reach. These patterns

related to measured morphological differences between *P. fremontii* between reaches (Busch and Smith 1995). In the gaining reach, the trees had greater stem elongation, leaf number, and leaf area. Others have measured smaller leaf size, decreased annual stem elongation, and reduced radial stem increments on water stressed cottonwoods (Smith et al., 1991, Stromberg and Patten, 1991; Busch and Smith, 1995, Scott et al. 1999). Cottonwoods also sacrifice branches in response to drought stress (Rood et al. 2000a). Genetic research suggests that trees locally adapt to moisture gradients, with mesic genotypes having increased height and diameter growth (Dunlap et al. 1994).

Cottonwood seedlings, though not measured in this study, may be affected by the lower water tables in the losing reach. Seedlings of *P. deltoides* have been shown to survive to a water table depth of 80 cm in coarse soil after one growing season (Segelquist et al.1993). According to the recruitment box model for cottonwood survival (Mahoney and Rood 1998), stream declines of 0.5-1 cm/day combined with root growth of 0.5-1 cm/day are required for seedling survival, and seedling roots may grow up to 100 cm in the first year. Seedlings in the losing reach of Nyack would have experienced water table declines that exceeded 150 cm by the end of the growing season in the losing reach (Fig. 8). In the gaining reach, the cottonwoods may have benefited from elevated water tables supported by inflowing ground water. Cottonwoods also might have benefited from increased soil moisture within preferential flow paths, such as in paleochannels, in the losing reach. With increased root water availability, cottonwood trees in gaining reach or near preferential flow paths may have allocated more carbon to above-ground growth, rather than below-ground growth to access limited water (Pregitzer and Friend 1996). Such growth allocations in response to variations in rates of water table declines have been measured in cottonwood seedlings (Rood et al. 2000b).

Substrate texture also may have influenced growth rates, either directly by altering available soil moisture, or indirectly by favoring other plant species and/or different reproductive strategies of the cottonwoods. Within reaches, soil textures varied surrounding deposits of wood (Mouw et al. 2001). As fine sediments tend to be deposited downstream of wood (Abbe and Montgomery 1996), these sites would be conducive to seedling establishment, both by providing protection from flood scour and by increasing the capillary fringe in the finer soil (Mahoney and Rood 1992). The presence of finer textured soils, such as those surrounding wood debris, may affect cottonwoods differently at sites with contrasting hydrology. For example, in a strongly losing reach, fine soils would increase the capillary fringe, thus increasing soil moisture available to roots. Conversely, on sites with a high water table, fine substrates may lead to saturated conditions that are not preferred cottonwood sites, but rather more suited for *Salix* or *Alnus* species.

Soil textures that retain water and nutrients may favor mesic plants (Merigliano 1996). Cottonwood growth might increase in response to the increased availability of water and nutrients. Alternatively, variations in understory composition may indirectly benefit cottonwood trees by changing the vegetation composition in the understory. On Nyack, the fastest growing cottonwoods (plots 20 and 21, see Fig. 3 for location) occurred in the gaining reach in plots with relatively low cottonwood density. While understory communities were not formally surveyed in this study, field notes and photographs suggested that plants more tolerant of saturated soils, such as red-osier dogwood (*Cornus stolonifera*), alder (*Alnus spp.*), and willow (*Salix spp.*) were abundant in the understories. Fine-textured, moist soils in the gaining reach may have encouraged the establishment of alder and willow at the same time as cottonwood establishment.

Increased competition from surrounding shrubs may have inhibited cottonwood seedlings. However, the surviving cottonwoods may have been more productive due to increased availability of sunlight (due to reduced cottonwood density) once the tree canopy rises above the shrub layer. Alternatively, inundation and soil saturation in the lower floodplain may have favored asexual reproduction (Krasny et al. 1988a). Root suckering has been found to negatively correlate with total stem density of genets (Krasny et al. 1988b), so perhaps the interaction of site conditions favorable to asexual reproduction may lead to lower densities, thus contributing to the increased growth.

Tree gender, though not measured, may provide an alternative explanation to growth variations. Grant and Mitton (1979) found female aspen trees to have higher vegetative growth rates (measured as stem diameter) compared to males, and male trees were more common at higher elevations where physical stress was greater. Similar studies of variations in cottonwood growth between sexes in relation to environmental stress have yet to be conducted, though Comtois et al. (1986) found that for *P. balsamifera*, male trees occurred with higher frequency on extreme sites, and female trees occurred on protected, nutrient-rich sites. Variations in water and nutrient availability between the gaining and losing reaches may influence sex ratios of black cottonwoods, and tree growth may differ between sexes.

Along with differences between growth of cottonwoods, soil protein concentrations differed between the floodplain reaches, with increased concentrations present in the gaining reach. An explanation for the abundance of the protein in the gaining reach could not be determined from the study. Differences in plant species composition, soil type, water and nutrient availability may influence AM fungi that produce the protein, or other root exudates may be involved. Possibly, increased

productivity of vegetation, such as in the gaining reach, leads to increased carbon availability for AM fungi that produce protein. Protein from fungi, or possibly other root exudates, living in association with cottonwood trees may have far-reaching influences on the ecosystem in terms of the stability (Tisdall and Oades 1982, Tisdall et al. 1997, Wright and Upadhyaya 1998) and nutrient stores (De Freitas et al. 1996, Andrade et al. 1998) in soils.

*Factors influencing the distribution of cottonwood trees*

Flood scour and deposition associated with channel avulsions and peak flows interacted to determine cottonwood establishment and distribution on the Nyack Flood Plain. This suggested that cottonwoods required channel avulsions to scour sites and deposit sediments for establishment, as well as to leave subsurface flow paths where water is focused and available to vegetation. In the losing reach, scouring appeared greater after the 1964 compared to the gaining reach (Fig. 2 and 3). Furthermore, the channel moved more in the losing reach (Fig. 14) compared to the gaining reach (Fig. 15). The scouring and deposition associated with channel avulsions, particularly in the losing reach, likely created bare sites conducive to seedling establishment (Braatne et al. 1996). However, reduced availability of water in the losing reach may have limited seedling establishment to high discharge years.

Variability of ages within plots and patterns of establishment in average discharge years (Fig. 13) suggested asexual reproduction occurred on Nyack. Age heterogeneity may represent the presence of root suckers, stump sprouts, different depths of sediment at the trunk bases, or errors in ring counts, due to missing or double rings. Black cottonwoods clonally reproduce, so their establishment is not limited to years of floods

(Brayshaw 1965, Gom 1996). The type of reproduction likely affects the stand structure of cottonwoods, but in this study, sexually versus asexually established trees were not differentiated, unless obvious. Krasny et al. (1988b) found that root suckering predominated on dry, sandy sites, and this may have occurred in the losing reach of Nyack. Deposition of wood and accumulation of fine soils (Abbe and Montgomery 1996), in areas such as the gaining reach of the floodplain, may lead to moister soils, as well as contribute to the deposition of nurse logs. Re-sprout growth following beaver felling may also affect measured tree age.

Cottonwood trees established adjacent to abandoned river channels (Fig. 14), suggesting that subsurface flow within these paths led to longer periods of water availability into the growing season *and* may have contributed nutrients. These paleochannels are distinct depressions in the floodplain landscape, so the water table is closer to the surface. The availability of water may be particularly important in the losing reach. When cottonwoods established in the losing reach, they grew above an area where the water table was low, unless they colonized in or beside an abandoned river channel. Cottonwoods that established *adjacent* to, but not directly in, old channels, may have benefited from ground water routing through these channels without suffering from the flood scour or mesic soil that occur in the bottom of the paleochannels.

The presence of faster growing cottonwoods in the vicinity of paleochannels and in the gaining reach suggested that cottonwoods responded to groundwater flow paths. Cottonwoods established and grew preferentially where interstitial flow was near the surface. Processes that maintain interstitial flows, particularly channel avulsions, are crucial for cottonwood life histories because these disturbances create sites for seed

germination and also leave subsurface flow paths where water, and possibly nutrients, are focused and available to vegetation.

## Literature Cited


Abbe, T.M. and D.R. Montgomery. 1996. Large woody debris jams, channel hydraulics, and habitat formation in large rivers. Regulated River Research and Management 12: 201-221.

Andersen, D.C. and D.J. Cooper. 2000. Plant-herbivore-hydroperiod interactions: effects of native mammals on floodplain tree recruitment. Ecological Applications 10:1384-1399.

Andersen, D.C., K.R. Wilson, M.S. Miller, M. Falck. 2000. Movement patterns of riparian small mammals during predictable floodplain inundation. Journal of Mammalogy 81(4):1087-1099.

Andrade, G., K. Mihara, R. Linderman, G. Bethlenfalvay. 1998. Soil aggregation status and rhizobacteria in the mycorrhizosphere. Plant and Soil. 202:89-96.

Armour, C.L. D.A. Duff, and W. Elmore. 1991. The effects of livestock grazing on riparian and stream ecosystems. Fisheries 16:7-11.

Bansak, T.S. 1998. The influence of vertical hydraulic exchange on habitat heterogeneity and surficial primary production on a large alluvial flood plain of the Middle Fork Flathead River. M.S. Thesis. The University of Montana, Missoula. 68 pp.

Bechtold, J.S. 2000. Successional controls on nitrate leaching from a flood-plain forest. M.S. Thesis. University of Washinton, Seattle, WA.

Bilby, R.E. and P.A. Bisson. 1998. Function and distribution of large woody debris. Pages 324-346 in Naiman, R.J., Bilby, R.E. eds. River Ecology and Management: Lessons from the Pacific Coastal Ecoregion. New York: Springer-Verlag.

Boulton, A.J. S. Findlay, P. Marmonier, E.H. Stanley, and H.M. Valett. 1998. The functional significance of the hyporheic zone in streams and rivers. Annual Review of Ecological Systems 29:59-81.

Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. *In* Biology or *Populus* and its implications for management and conservation. Part I, Chapter 3. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. pp. 57-85.

Brayshaw, T.C. 1965. The status of the black cottonwood (*Populus trichocarpa* Torrey and Gray). Canadian Field-Naturalist 79:91-95.

Busch, D.E. and S.D. Smith. 1995. Mechanisms associated with decline of woody species in riparian ecosystems of the southwestern U.S.. Ecological Monographs. 65:347-370.

Carothers, S.W., R.R. Johnson, and S.W. Aitchison. 1974. Population structure and social organization of southwestern riparian birds. American Zoologist 14:97-108.

Cavallo, B.J. 1997. Floodplain habitat heterogeneity and the distribution, abundance, and behaviour of fishes and amphibians in the Middle Fork Flathead River Basin, Montana. M.S. Thesis. The University of Montana, Missoula. 128pp.

Comtois, P., J.P. Simon, S. Payett. 1986. Clonal constitution and sex ratio in northern populations of balsam poplar, *Populus balsamifera*. Holarctic Ecology 9:251-260.

Crouch, G.L. 1979. Long-term changes in cottonwoods on a grazed and an ungrazed plains bottomland in northeastern Colorado. USDA Forest Service Research Note RM-370 Fort Collins, Colorado.

Dahm, C.N., N.B. Grimm, P. Marmonier, H.M. Valett, P.Vervier. 1998. Nutrient dynamics at the interface between surface waters and groundwaters. Freshwater Biology 40:427-451.

De Freitas, P.L., R.W. Zobel, and V.A. Snyder. 1996. A method for studying the effects of soil aggregate size and density. Soil Society of America Journal 60:288-290.

Dunlap, J.M., P.E. Heilman, and R.F. Stettler. 1994. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. VII. Two-year survival and growth of native black cottonwood clones from four river valleys in Washington. Canadian Journal of Forest Research. 24:1539-1549.

Ellis, B.K., J.A. Stanford, and J.V. Ward. 1998. Microbial assemblages and production in alluvial aquifers of the Flathead River, Montana, USA. Journal of the North American Benthological Society. 17:382-402.

Fetherston, K.L., R.J. Naiman, R.E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Journal of Geomorphology 13:133-144.

Finch, D.M. and L.R. Ruggiero. 1993. Wildlife and biological diversity in the Rocky Mountains and north Great Plain. Natural Areas Journal 13:191-203.

Fleischner, T.L. 1994. Ecological costs of livestock grazing in Western North America. Conservation Biology 8:629-644.

Freitas, P.L. R.W. Zobel, and V.A. Snyder. 1996. A method for studying the effects of soil aggregate size and density. Soil Society of America Journal 60:288-290.

Galloway, G. and J. Worrall. 1979. Cladoptosis: a reproductive strategy in black cottonwood? Canadian Journal of Forest Research 9:122-125.

Gom, L.A. and S.B. Rood. 1999. Patterns of clonal occurance in a mature cottonwood grove along the Oldman River, Alberta. Canadian Journal of Botany 77:1095-1105.

Grant, M.C. and J.B. Mitton. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. Evolution 33:914-918.

Grimm, N.B. and S.G. Fisher. 1984. Exchange between surface and interstitial water: Implications for stream metabolism and nutrient cycling. Hydrobiologia 111:219-228.

Huggenberger, P., E. Hoehn, R. Beschta, W. Woessner. 1998. Abiotic aspects of channels and floodplains in riparian ecology. Freshwater Biology 40:407-425.

Jastrow, J.D., T.W. Boutton, and R.M. Miller. 1996. Carbon dynamics of aggregate-associated organic matter estimated by carbon-13 natural abundance. Soil Science Society of America Journal 60:801-808.

Johnston, C.A. and R.J. Naiman. 1990. Browse selection by beaver: effects on riparian forest composition. Canadian Journal of Forest Research 20:1036-1043.

Jones, J.B. and P.J. Mulholland. 2000. Streams and groundwaters. *in* J.H. Thorp (editor). Aquatic Ecology Series. Academic Press, San Diego, California.

Krasny, M.E., K.A. Vogt, and J.C. Zasada. 1988a. Establishment of four *Salicaceae* species on river bars in interior Alaska. Holarctic Ecology 11:210-219.

Krasny, M.E., J.C. Zasada, and K.A. Vogt. 1988b. Adventitious rooting of four *Salicaceae* species in response to a flooding event. Canadian Journal of Botany 66:2597-2598.

Lowrance, T. R. Todd, J. Fail, Jr., O. Hendrickson, Jr., R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. BioScience 34:374-377.

Mahoney, J.M. and S.B. Rood. 1992. Response of a hybrid poplar to water table decline in different substrates. Forest Ecology and Management 54:141-156.

Mahoney, J.M. and S.B. Rood. 1998. Streamflow requirements for cottonwood seedling recruitment--an integrative model. Wetlands 18:634-645.

Merigliano, M.F. 1996. Ecology and management of the South Fork Snake River cottonwood forest. Idaho BLM Technical Bulletin 96-9.

Mouw J. et al. 2001. Local influence to vascular plant diversity on floodplain landscapes: attaining an ecosystem perspective. *In review.*

Naiman, R.J., R.E. Bilby, and P. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. BioScience 50:996-1011

Pepin, D.M. and F.R. Hauer. 2001 *in review*. Benthic responses to groundwater-surface water exchange in two alluvial rivers.

Peterjohn, W.T. and D.L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observation of a riparian forest. Ecology 65:1466-1475.

Polzin, M.L. and S.B. Rood 2000. Effects of damming and flow stabilization on riparian processes and black cottonwoods along the Kootenay River. Rivers 7:221-232.

Poole, G.C., R.J. Naiman, J. Pastor, and J.A. Stanford. 1997. Uses and limitations of ground penetrating RADAR in two riparian systems. Pages 140-148 *in* J. Gibert, J. Mathieu and F. Fournier (editors). Groundwater/Surface Water Ecotones: Biological and Hydrological Interactions and Management Options. Cambridge University Press, Port Chester, New York.

Poole, G.C. 2000. Morphologic analysis and dynamic simulation of surface- and groundwater flux on a large alluvial flood plain. Ph.D. Dissertation. The University of Montana.

Poole, G.C., J.A. Stanford, S.W. Running, and C.A. Frissell. 2001 *in review*. Morphologic determinants of floodplain hydrology: 2) Local dynamics, preferential flow, and river regulation.

Pregitzer, K.S. and A.L. Friend. 1996. The structure and function of *Populus* root systems. *In* Biology or *Populus* and its implications for management and conservation. Part II, Chapter 14. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. pp. 331-354.

Rillig M.C., S.F. Wright, M.F. Allen, and C.B. Field. 1999. Rise in carbon dioxide changes soil structure. Nature 400, 628.

Rood, S.B. and S. Heinze-Milne. 1989. Abrupt downstream forest decline following river damming in southern Alberta. Canadian Journal of Botany 67:1744-1749.

Rood, S.B. and J.M. Mahoney. 1990. Collapse of riparian poplar forests downstream from dams in Western prairies: Probable cause and prospects for mitigation. Environmental Management 14:451-464.

Rood, S.B., S. Patino, K. Coombs, M.T.Tyree. 2000a. Branch sacrifice: cavitation-associated drought adaptation of riparian cottonwoods. Trees 14:248-257.

Rood, S.B., K. Zanewich, C. Stefura, and J.M. Mahoney. 2000b. Influence of water table decline on growth allocation and endogenous gibberellins in black cottonwood. Tree Physiology 20:831-836.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9:135-151.

Scott, M.L., J.M. Friedman, G.T. Auble. 1996. Fluvial process and the establishment of bottomland trees. Geomorphology 14:327-339.

Scott, M.L., P.B. Shafroth, and G.T. Auble. 1999. Responses of riparian cottonwoods to alluvial water table declines. Environmental Management 23:347-358.

Segelquist, C.A., M.L. Scott, and G.T. Auble. 1993. Establishment of Populus deltoides under simulated alluvial groundwater declines. American Midland Naturalist. 130:274-285.

Smith, S.D., A.B. Wellington, J.L. Nachlinger, and C.A. Fox. 1991. Functional responses of riparian vegetation to streamflow diversion in the Eastern Sierra Nevada. Ecological Applications 1:89-97.

Stanford, J.A. and A.R. Gaufin. 1974. The hyporheic corridor of two Montana Rivers. Science 185:700-702.

Stanford, J.A. and J.V. Ward. 1988. The hyporheic habitat of river ecosystems. Nature 335:64-66.

Stanford, J.A., and J.V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12:48-60.

Stanford, J.A., J.V. Ward, and B.K. Ellis. 1994. Ecology of the alluvial aquifers of the Flathead River, Montana (USA). Pages 367-390. *in* J. Gibert, D.L. Danielopol, and J.A. Stanford (editors). Groundwater Ecology. Academic Press, San Diego, California.

Stanford, J.A. et al. 2001, B.K. Ellis, and 5 others. *In review.* Surface and ground water interactions drive habitat heterogeneity and biotic distributions within a montane flood plain. Ecological Applications.

Stromberg, J.C. and D.T.Patten. 1991. Instream flow requirements for cottonwoods at Bishop Creek, Inyo County, California. Rivers 2:1-11.

Tisdall, J.M. and J.M. Oades. 1982. Organic matter and water-stable aggregates in soils. Journal of Soil Science 33:141-163.

Tisdall, J.M., S.E. Smith, and P. Rengasamy. 1997. Aggregation of soil by fungal hyphae. Australian Journal of Soil Research 35:55-60.

Triska, F.J. J.H. Duff, R.J. Avanzino. 1993. Patterns of hydrological exchange and nutrient transformation in the hyporheic zone of a gravel-bottom stream: Examining terrestrial-aquatic linkages. Freshwater Biology 29:259-274.

Valett, H.M., S.G. Fisher, N.B. Grimm, P. Camill. 1994. Vertical hydrological exchange and ecological stability of a desert stream ecosystem. Ecology 75:548-560.

Valett, H.M., C.N. Dahm, M.E. Campana, J.A. Morrice, M.A. Baker, and C.S. Fellows. 1997. Hydrologic influences on groundwater-surface water ecotones: Heterogeneity in nutrient concentration and retention. Journal of the North American Benthological Society 16:239-247.

Wallace, J.B., S.L. Eggert, J.L. Meyer, and J.R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Whitham, T.G., G.D. Martinsen, K.D. Floate, H.S. Dungey, B.M. Potts, and P. Keim. 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. Ecology 80:416-428.

Wondzell, M. 1992. Vegetation patterns along the Middle Fork of the Flathead River, Glacier National Park, Montana. M.S. Thesis. Colorado State University, Fort Collins. 243 pp.

Wright, S.F. and A. Upadhyaya. 1996. Extraction of an abundant and unusual protein from soil and comparison with hyphal protein of arbuscular mycorrhizal fungi. Soil Science 161:575-586.

Wright, S.F. and A. Upadhyaya. 1998. A survey for aggregate stability and glomalin, a glycoprotein produced by hyphae of arbuscular mycorrhizal fungi. Plant Soil 198:97-107.

Wright S. F., J.L. Star, and I.C. Paltineanu. 1999. Changes in aggregate stability and concentration of glomalin during tillage management transition. Soil Science Society of America Journal 63:825-1829.

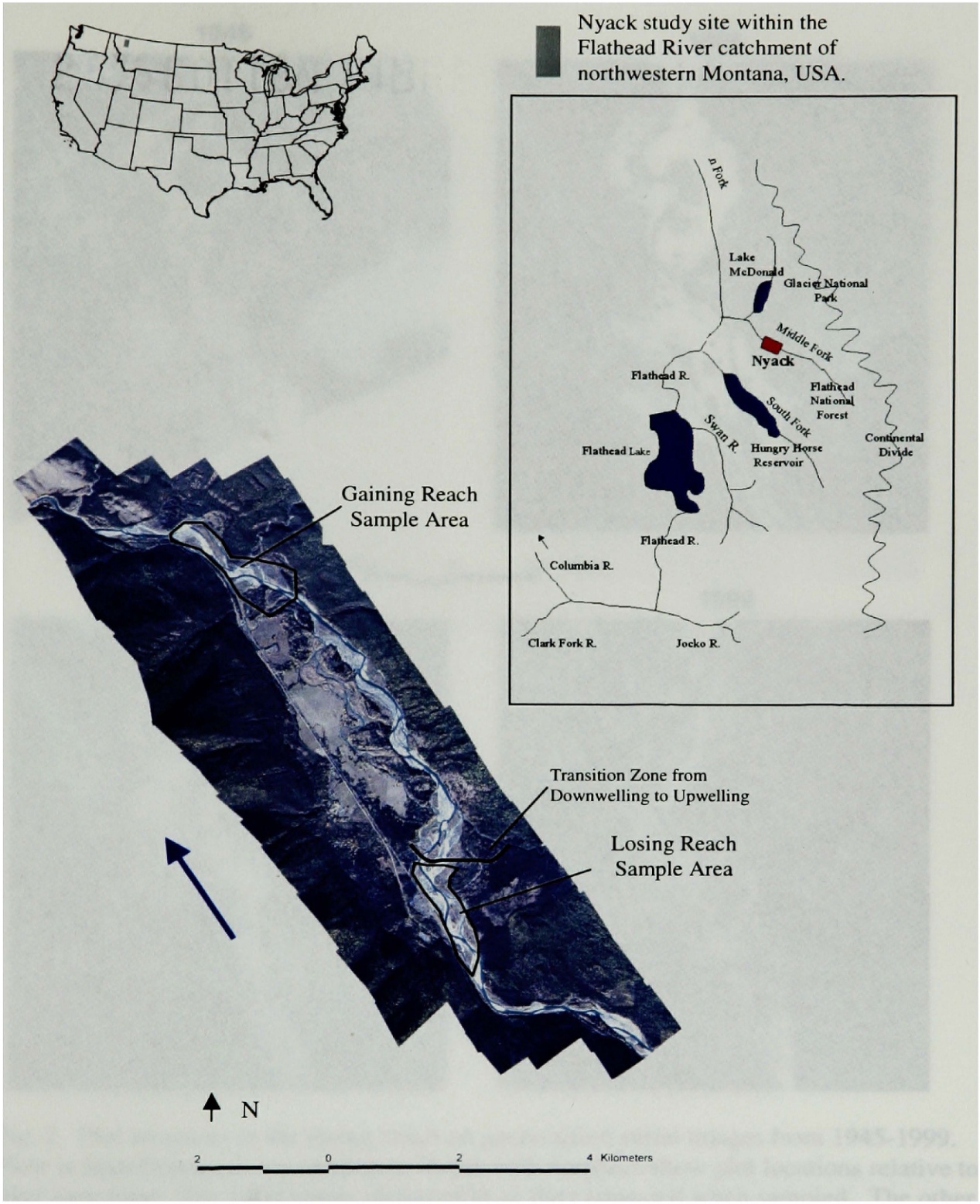


Fig. 1. Study site on Nyack Flood Plain of the Middle Fork of the Flathead River. Surface waters enter the alluvial aquifer at the upstream end of the flood plain (bottom of photo). Ground water upwells throughout the flood plain via spring brooks and inflow to the channels. Plots were established within the circled areas in losing and gaining reaches.

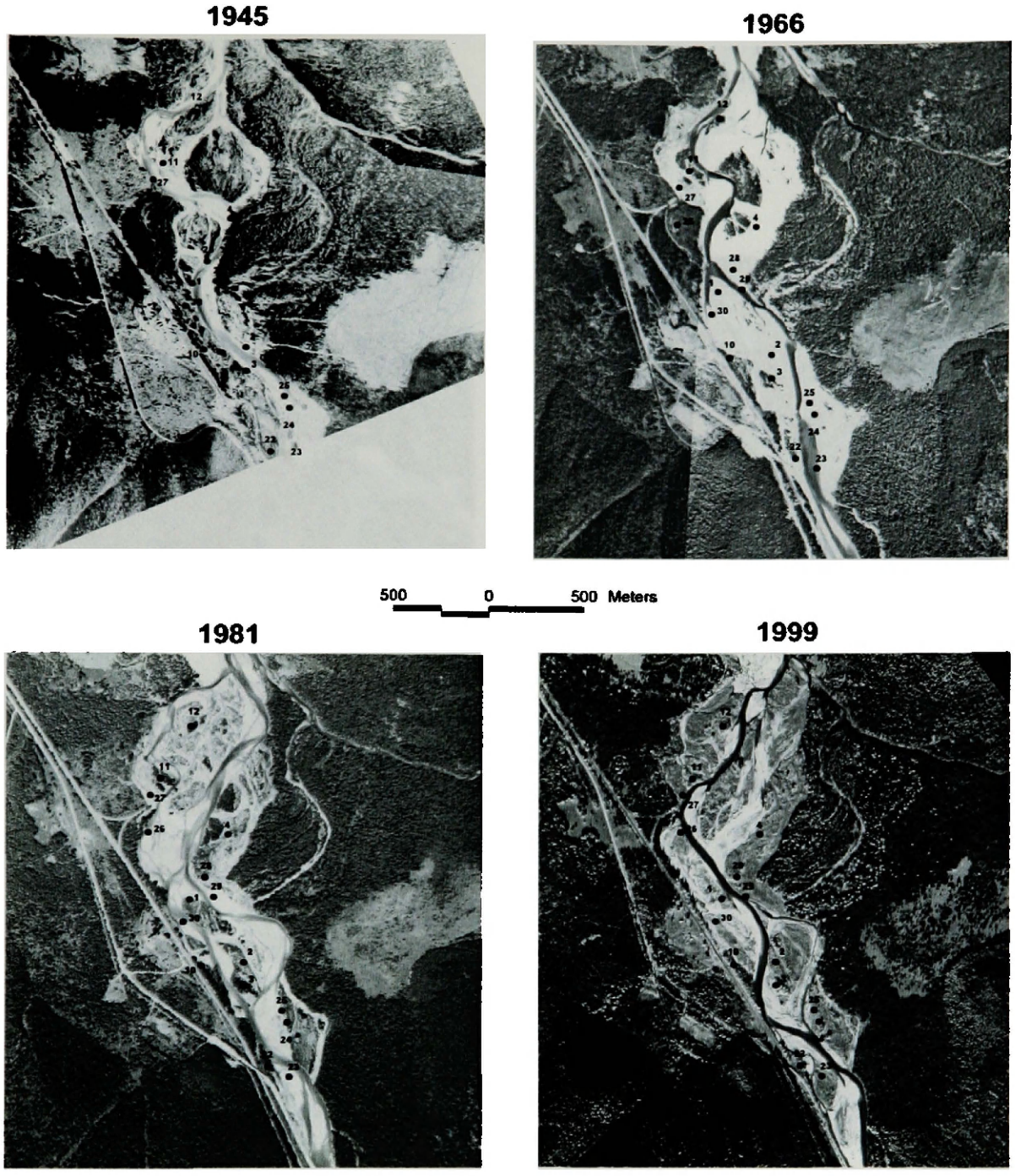


Fig. 2. Plot locations in the losing reach on georectified aerial images from 1945-1999. Flow is from bottom to top of photos. Points with numbers show plot locations relative to river over time. The 1999 image shows plots as they appeared when sampled. The other images represent those locations through time. For example, plot 11 (river left) did not exist in 1945, as the point is in the middle of the channel. By 1966 some vegetation had colonized the site. By 1981 the vegetation patch appears dense (mature forest). In 1999, the patch remains, but a channel avulsion has exposed the area to erosion.

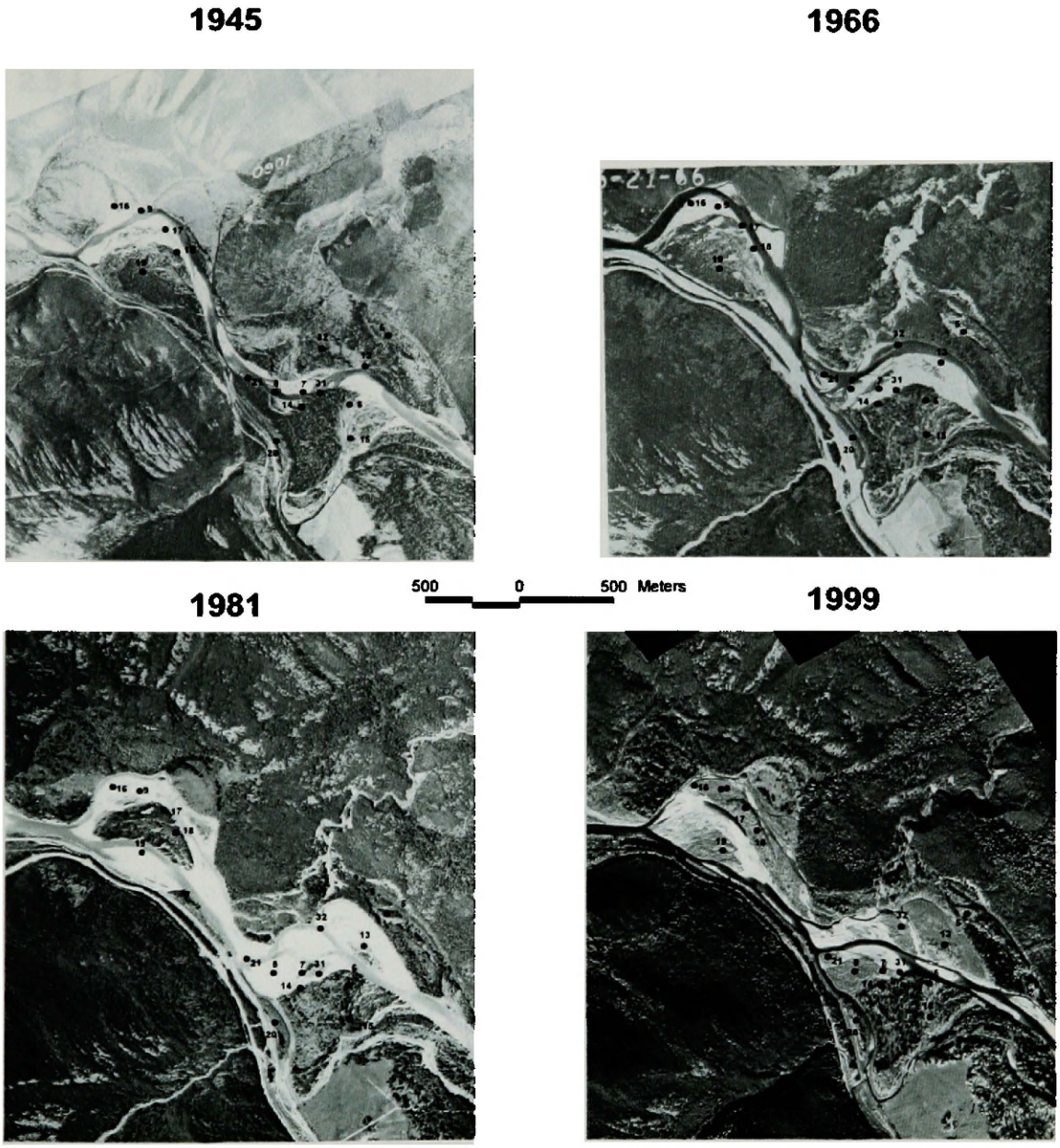


Fig. 3. Plot locations in the gaining reach on georectified aerial images from 1945-1999. Flow is from right to left. The photos were taken mid-late summer at the following discharges: 1945=22$m^3$/s; 1966=28 $m^3$/s and 228 $m^3$/s (photos taken on different days); 1981=132 $m^3$/s; and 1999=52 $m^3$/s.

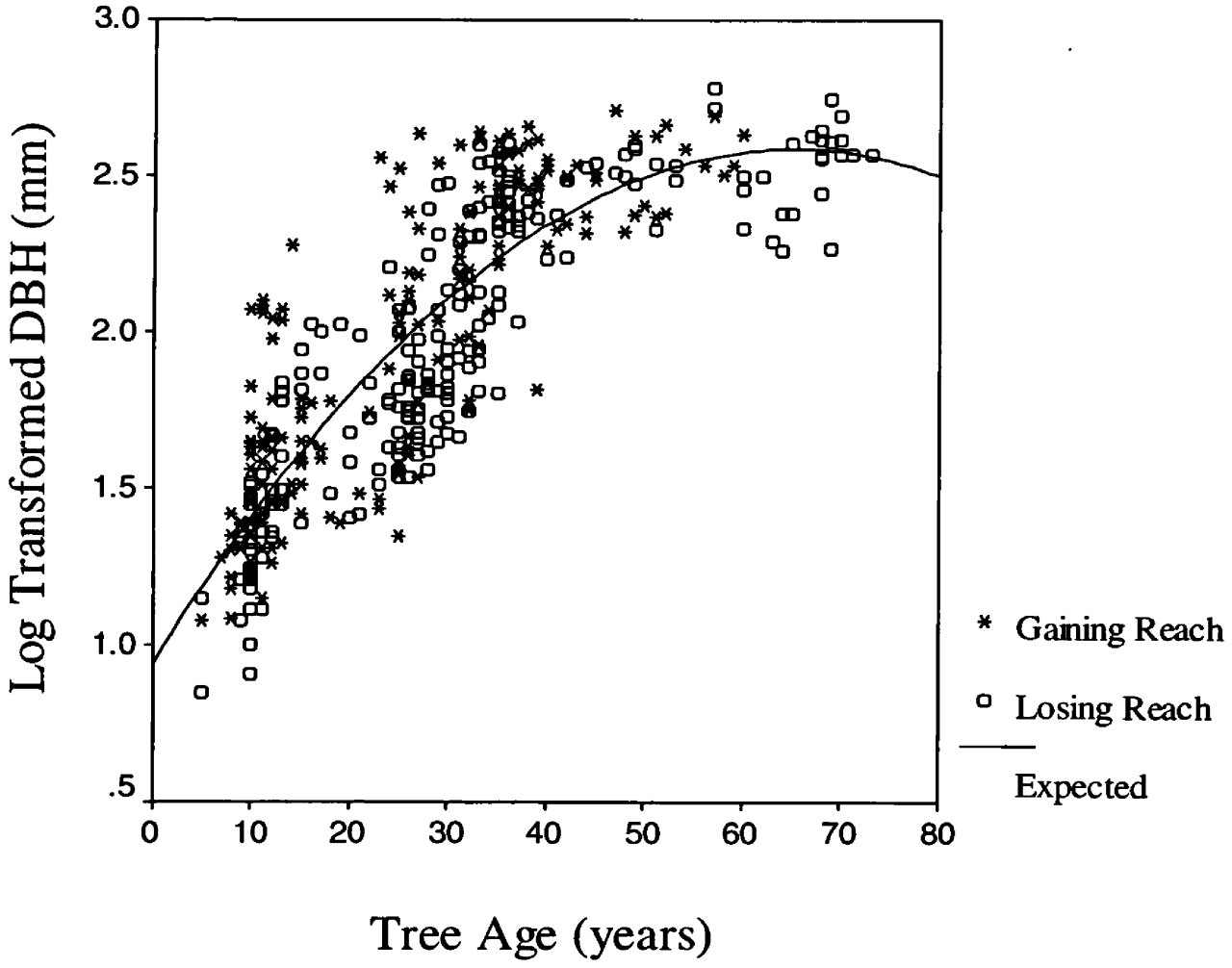


Fig. 4. Diameter at breast height related to tree age. The points represent individual trees (n = 402) from both the losing and gaining reaches. The line is the average tree diameter at a given age. The residuals (a point's deviation from the average) were used to calculate growth rate indices (see text). Note that DBH was log transformed to homogenize variance.

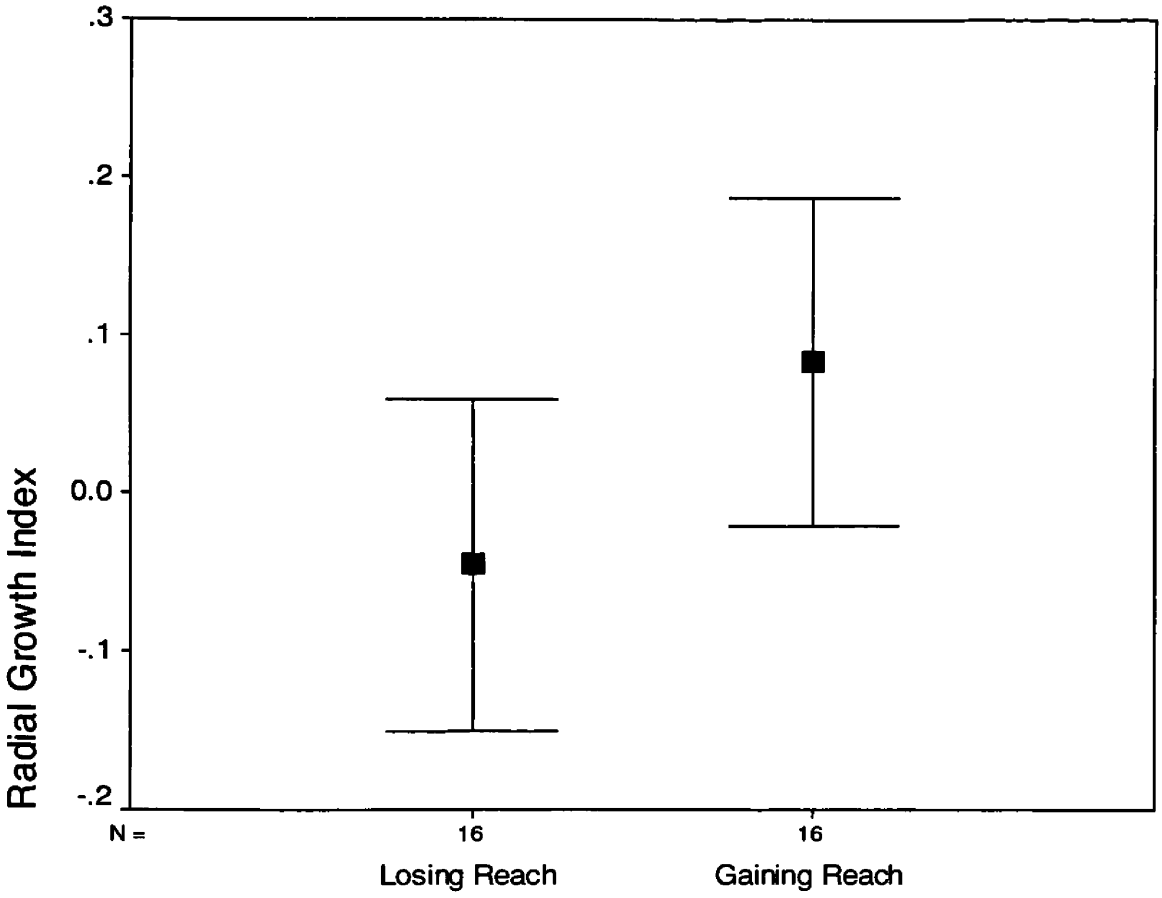


Fig. 5. Mean of growth rate indices for plots in the losing and gaining reaches of the flood plain. Bars represent 95% confidence intervals of the mean. See text and Fig. 4 for calculations of growth indices.

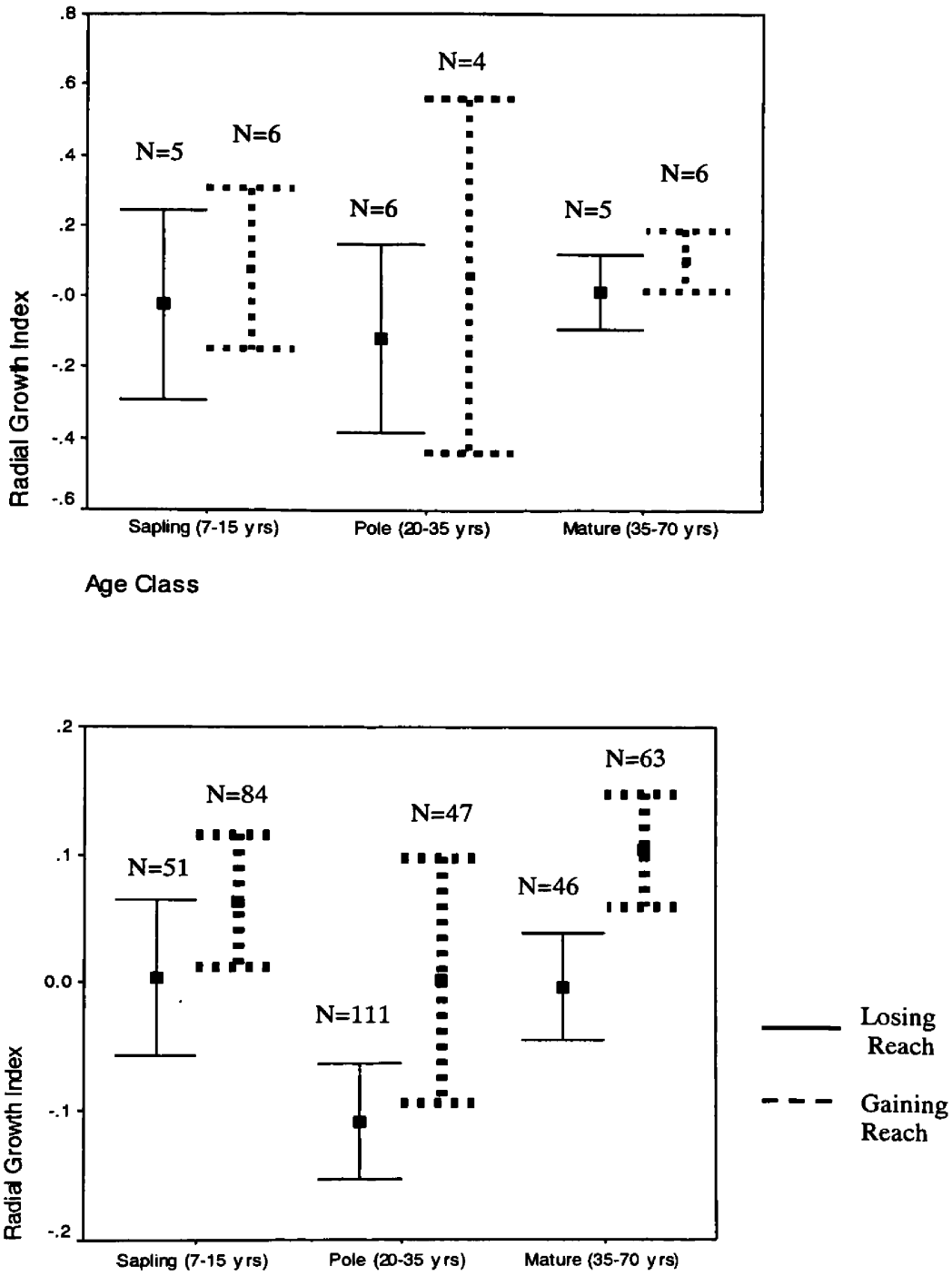


Fig. 6. Tree growth rate indices compared within stand types between reaches. Average growth within a plot is represented by the top graph. The bottom graph represents mean tree growth for all trees (not divided by plot) between stand types. Bars represent 95% confidence intervals of the mean.

| Method of Growth Analysis | Position | N | Mean | Std. Dev. | Sig. (2-tailed) |
|---|---|---|---|---|---|
| Growth Rate Index (calculated over entire life of tree) | Losing Reach | 16 | -0.045 | .1967 | 0.072 |
| | Gaining Reach | 16 | 0.084 | .194 | |
| 10 yr BA Growth/tree ($m^2$) | Losing Reach | 16 | 7601.71 | 7409.09 | 0.260 |
| | Gaining Reach | 15 | 13495.51 | 18262.17 | |
| 10 yr BA Growth/plot ($m^2$/ha) | Losing Reach | 16 | 22.24 | 22.24 | 0.623 |
| | Gaining Reach | 15 | 19.07 | 11.91 | |

Table 1. Average growth rates (based on 3 different calculations) compared between the losing and gaining reaches. Growth rate index is based on the relationship between DBH and tree age (Fig. 4). Ten-year basal area growth per tree and per plot are also presented.

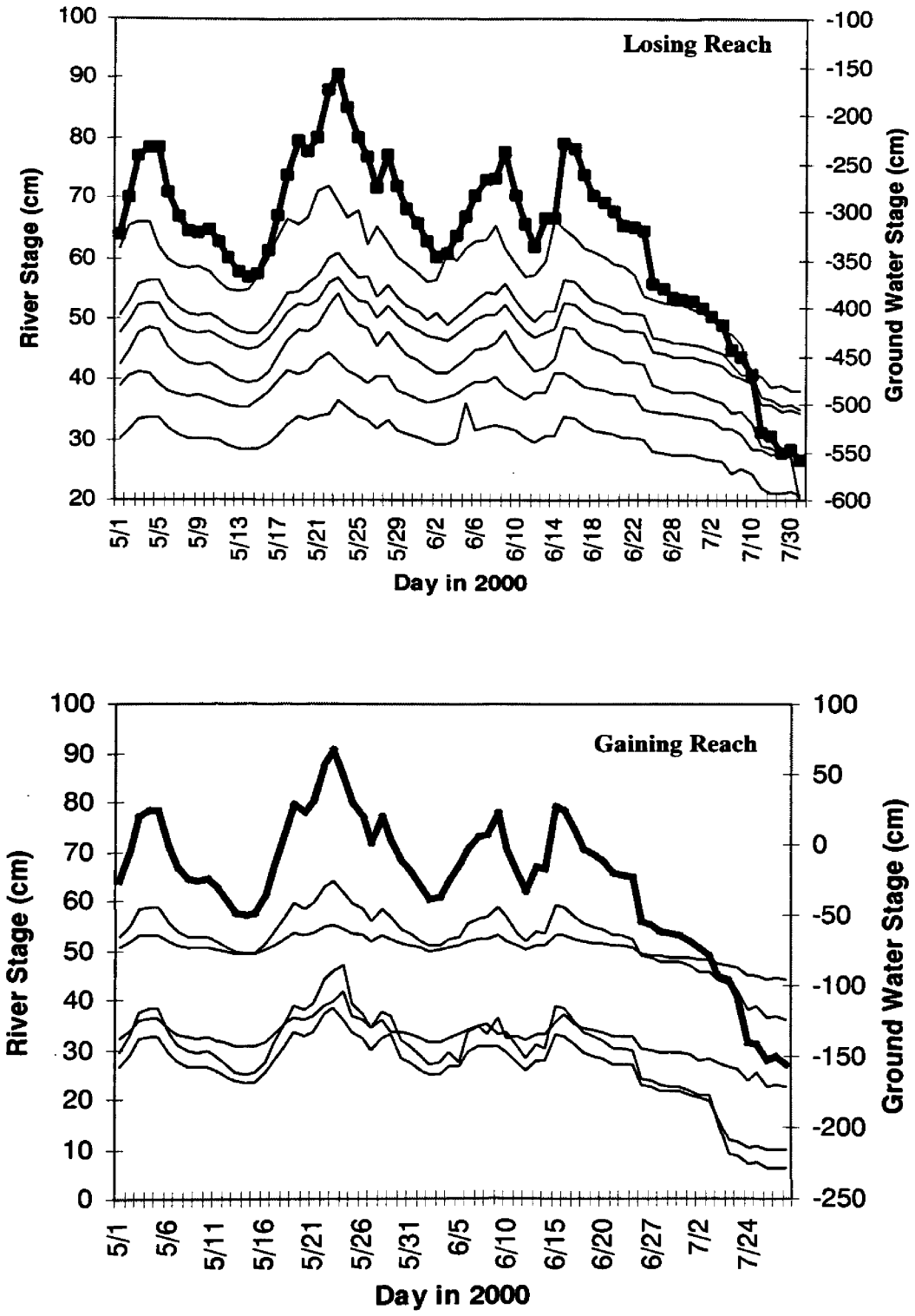


Fig. 7. Comparison of river stage and water table elevation through the growing season in the losing (top) and gaining (bottom) reaches. The darker lines represent river stage measured with a continuously recording depth sensor. Fine lines represent water table elevations measured within piezometers.

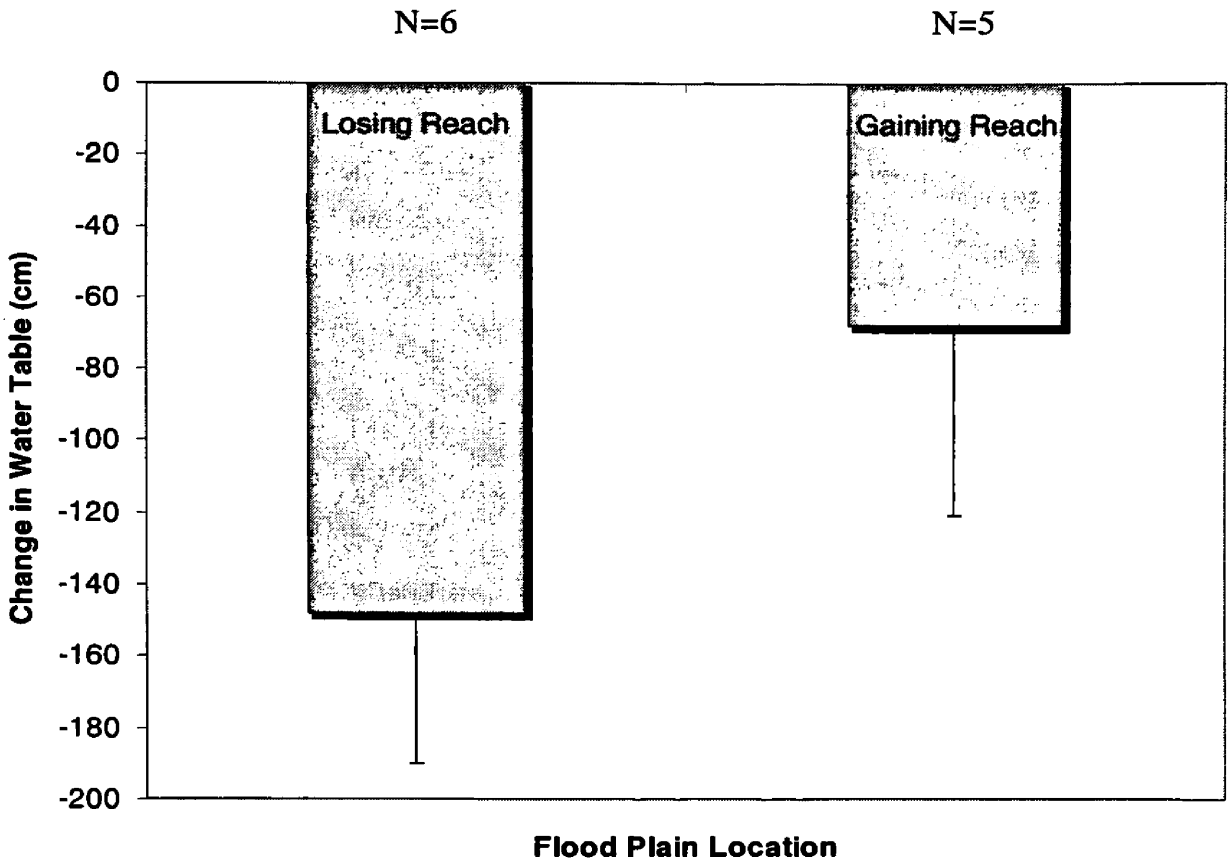


Fig. 8. Mean (-1SD) change in water table elevation in the losing and gaining reaches between peak discharge (Q = 424$m^3$/s) and approaching base flow (Q = 18$m^3$/s). Stage was measured in a total of 11 piezometers.

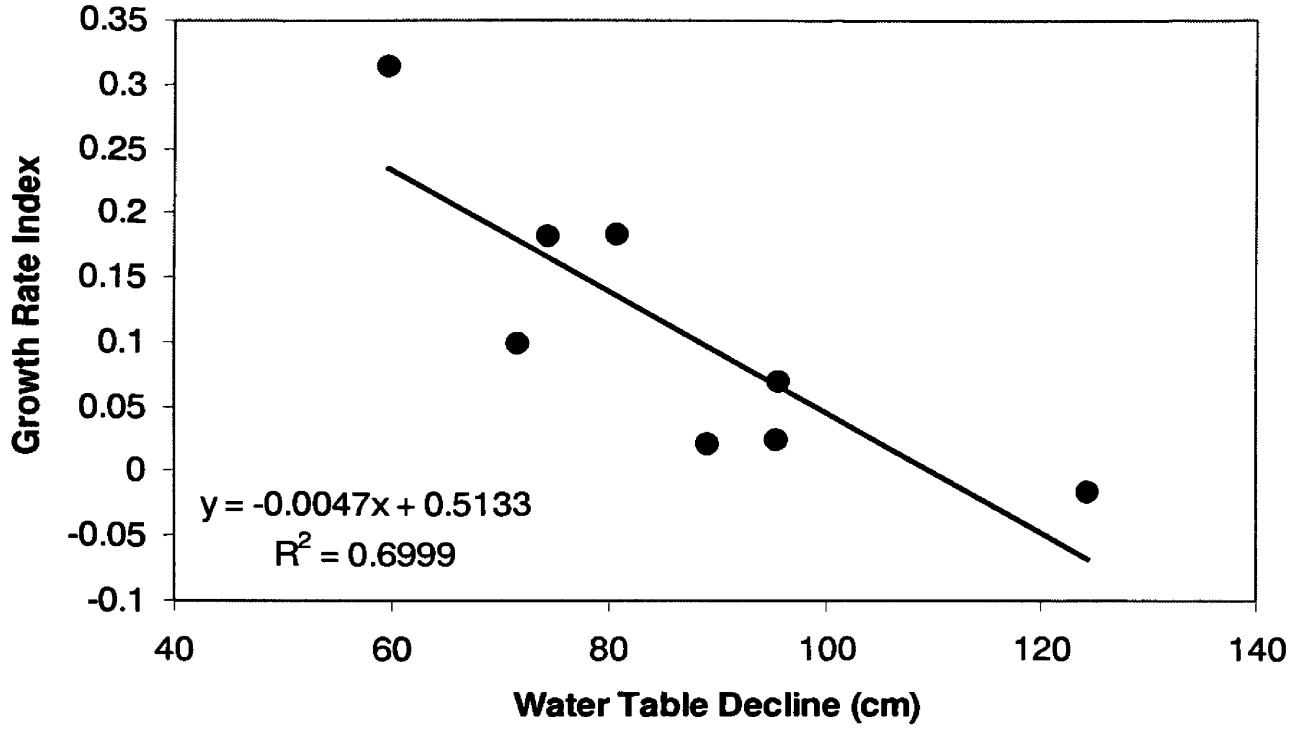


Fig. 9. Tree growth rate compared to change in water table elevation. Growth rate indices were determined using residuals from the relationship of tree diameter to tree age (Fig. 4). Water table elevations were measured in piezometers through one growing season.

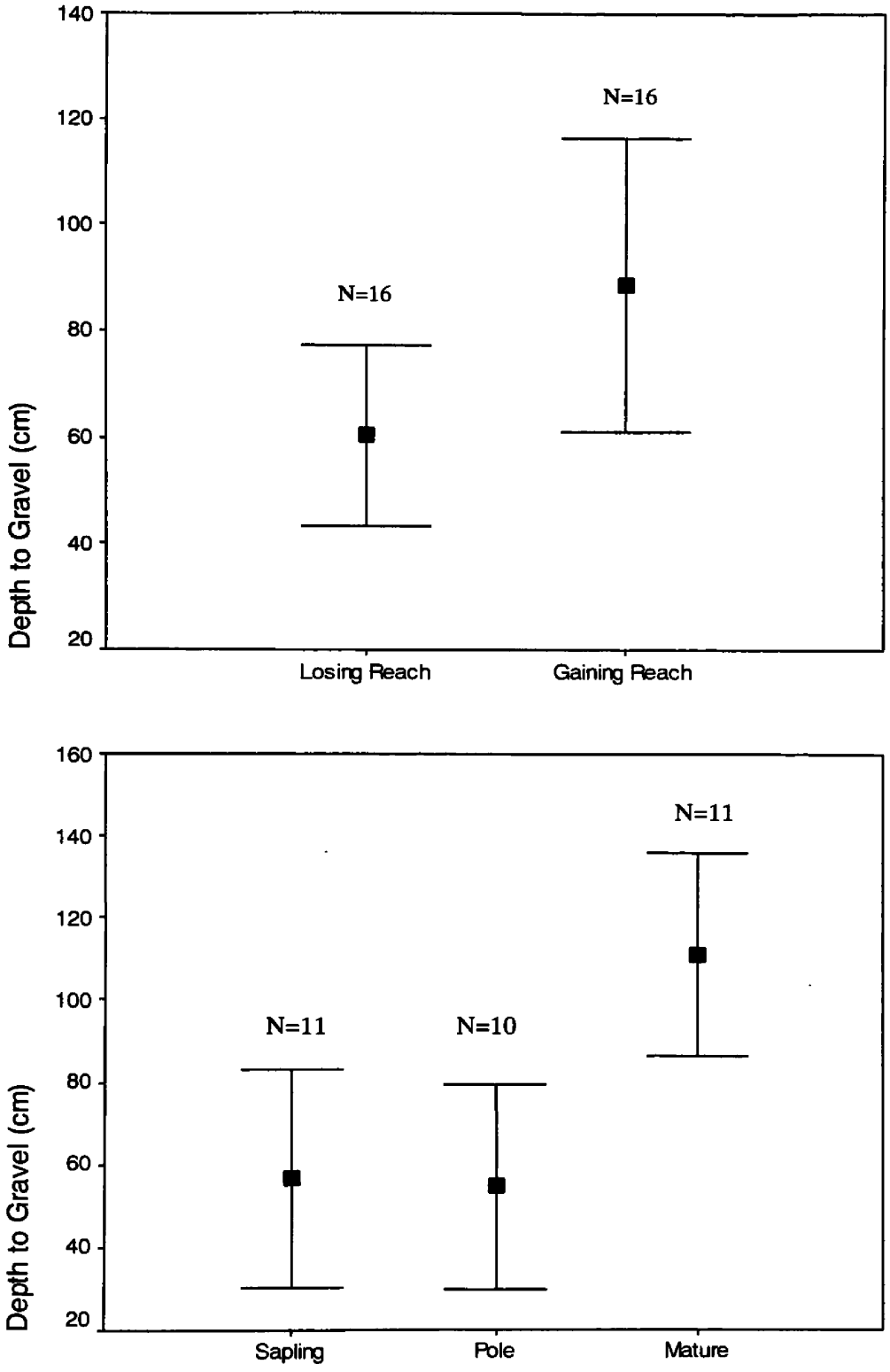


Fig. 10. Average depth to gravel in the losing and gaining reaches (top) and within age categories (bottom). Bars show 95% confidence limits of the mean.

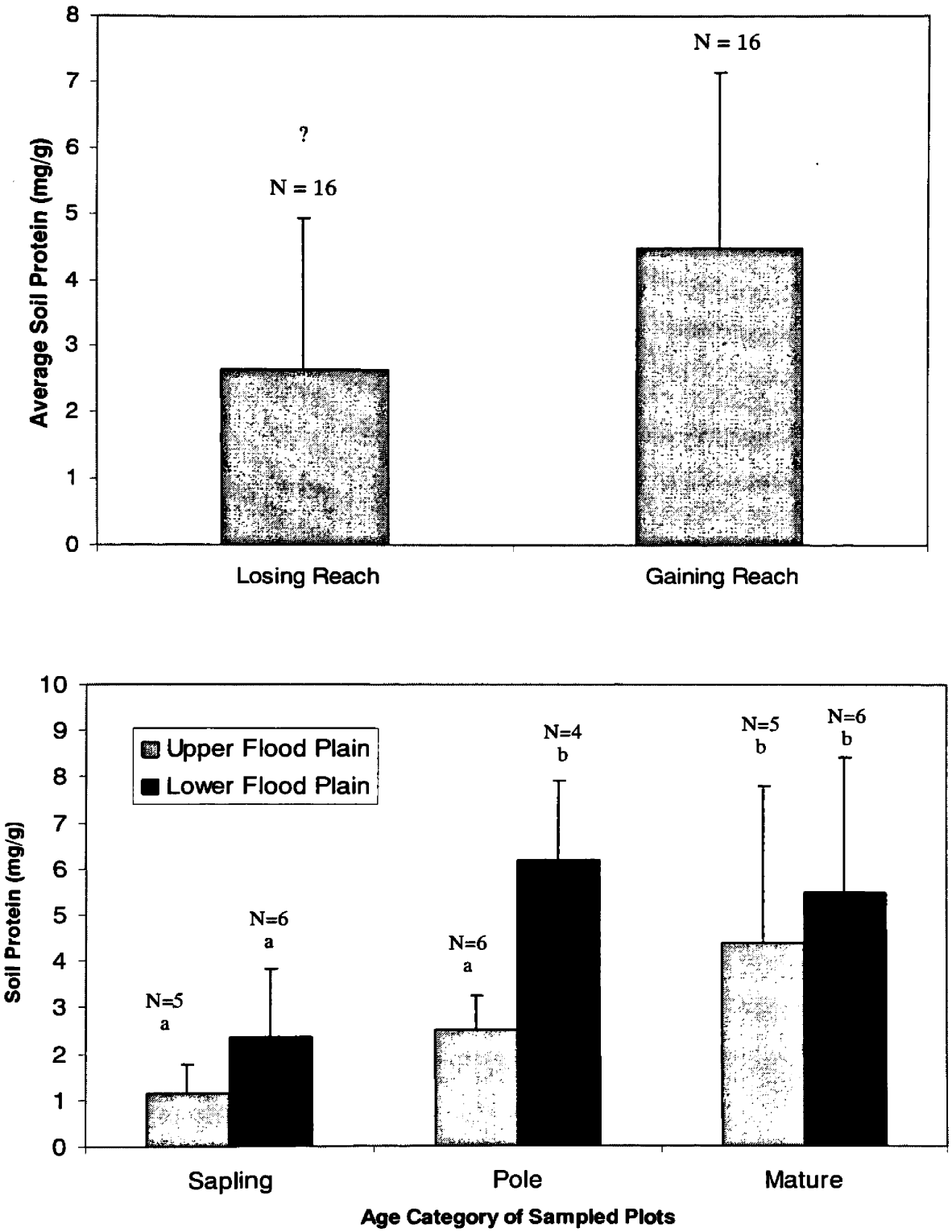


Fig. 11. Mean (+ 1 SD) protein concentrations compared between A horizons of losing and gaining reach plots (top) and within stand types between the upper (losing) and lower (gaining) reaches (bottom graph). Categories with different lower case letters are significantly different.

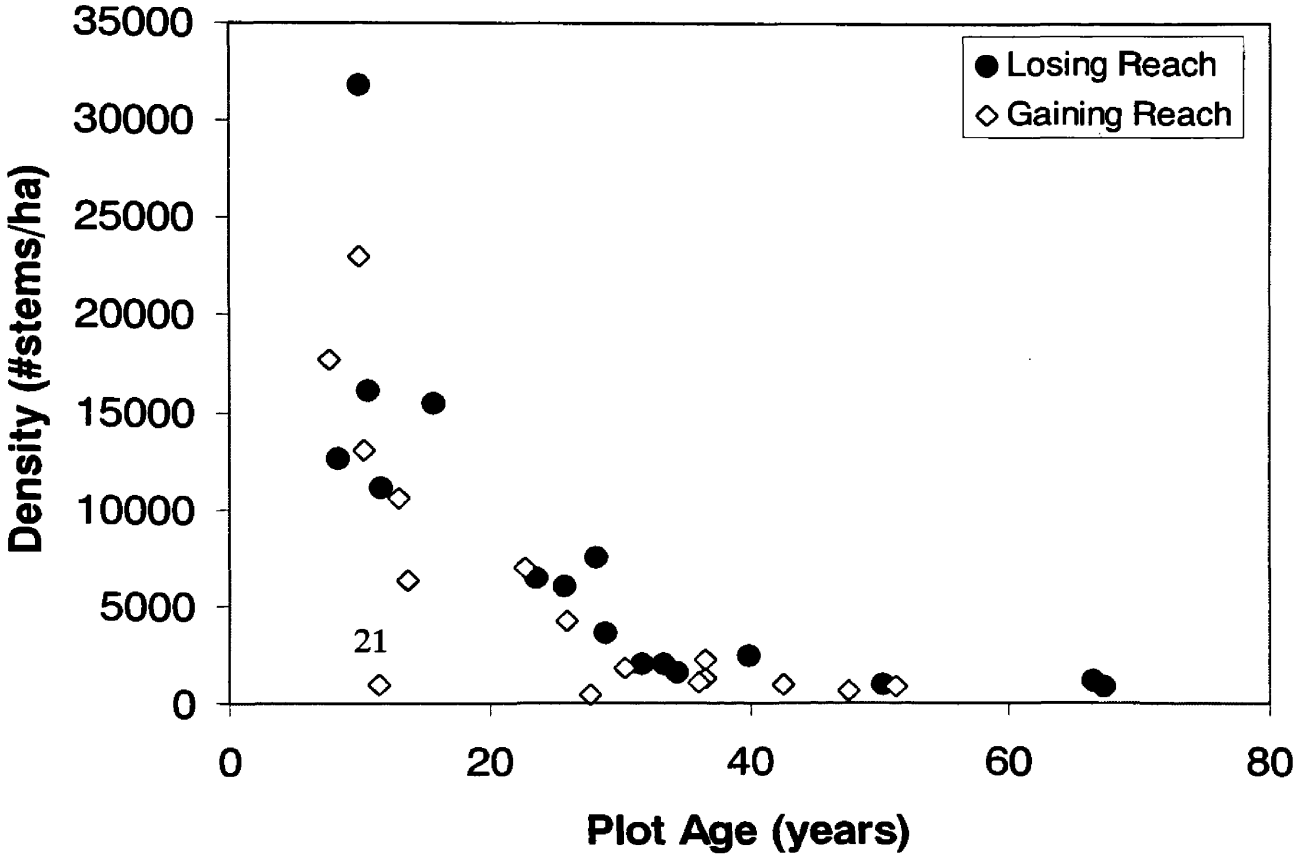


Fig. 12. Relationship between cottonwood stem density and plot age.

## Dependent Variable: Growth Rate Index

| Source | df | F | Sig. |
|---|---|---|---|
| Corrected Model | 5 | 2.696 | 0.043 |
| Intercept | 1 | 1.250 | 0.274 |
| Density | 1 | 0.922 | 0.346 |
| Depth to gravel | 1 | 2.346 | 0.138 |
| Elevation above Base flow | 1 | 4.002 | 0.056 |
| Concentration of Protein | 1 | 0.012 | 0.914 |
| Floodplain Position | 1 | 1.405 | 0.247 |

R Squared = 0.341

## Dependent Variable: 10 year BA Growth/tree ($m^2$)

| Source | df | F | Sig. |
|---|---|---|---|
| Corrected Model | 5 | 3.094 | 0.026 |
| Intercept | 1 | 2.991 | 0.096 |
| Density | 1 | 3.059 | 0.093 |
| Depth to gravel | 1 | 1.040 | 0.317 |
| Elevation above Base flow | 1 | 3.193 | .086 |
| Concentration of Protein | 1 | 0.642 | 0.430 |
| Floodplain Position | 1 | 0.047 | 0.830 |

R Squared = 0.382

## Dependent Variable: 10 year BA Growth/plot ($m^2$/ha)

| Source | df | F | Sig. |
|---|---|---|---|
| Corrected Model | 5 | 1.003 | 0.424 |
| Intercept | 1 | 7.308 | 0.012 |
| Depth to gravel | 1 | 0.548 | 0.466 |
| Elevation above Base flow | 1 | 2.517 | 0.125 |
| Concentration of Protein | 1 | 0.635 | 0.433 |
| Floodplain Position | 1 | 0.073 | 0.790 |

R Squared = 0.134

Table 2: Results of analysis of covariance for the three methods of growth analysis.

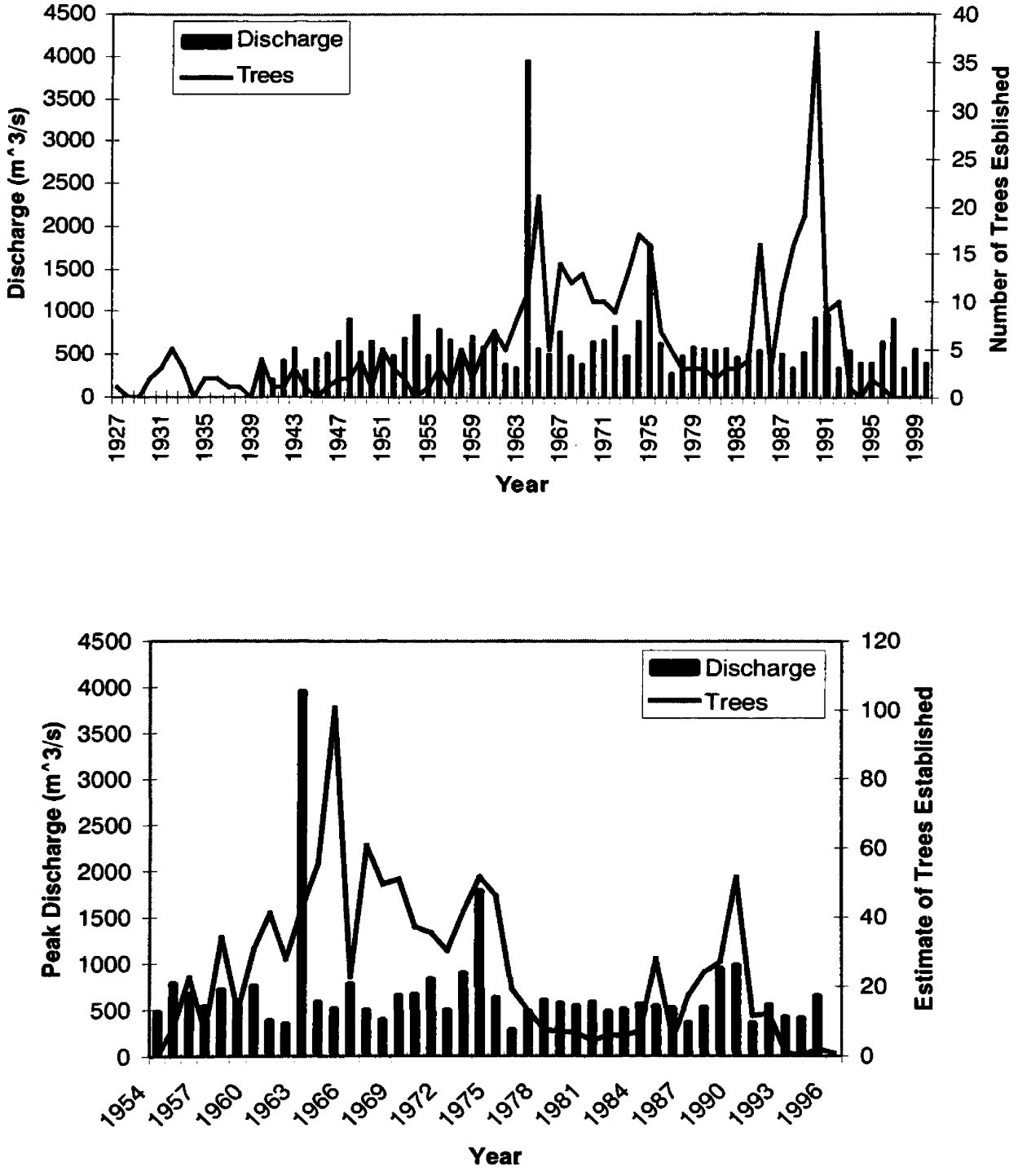


Fig. 13. Cottonwood establishment in relation to peak annual discharge. The top graph shows the number of trees measured in the sample (line) compared to the peak flow (bar) for all years of discharge record. The bottom graph represents an estimate of the number of trees established (line) based on tree mortality (calculated from density relationships, Fig. 12) compared to peak discharge (bars).

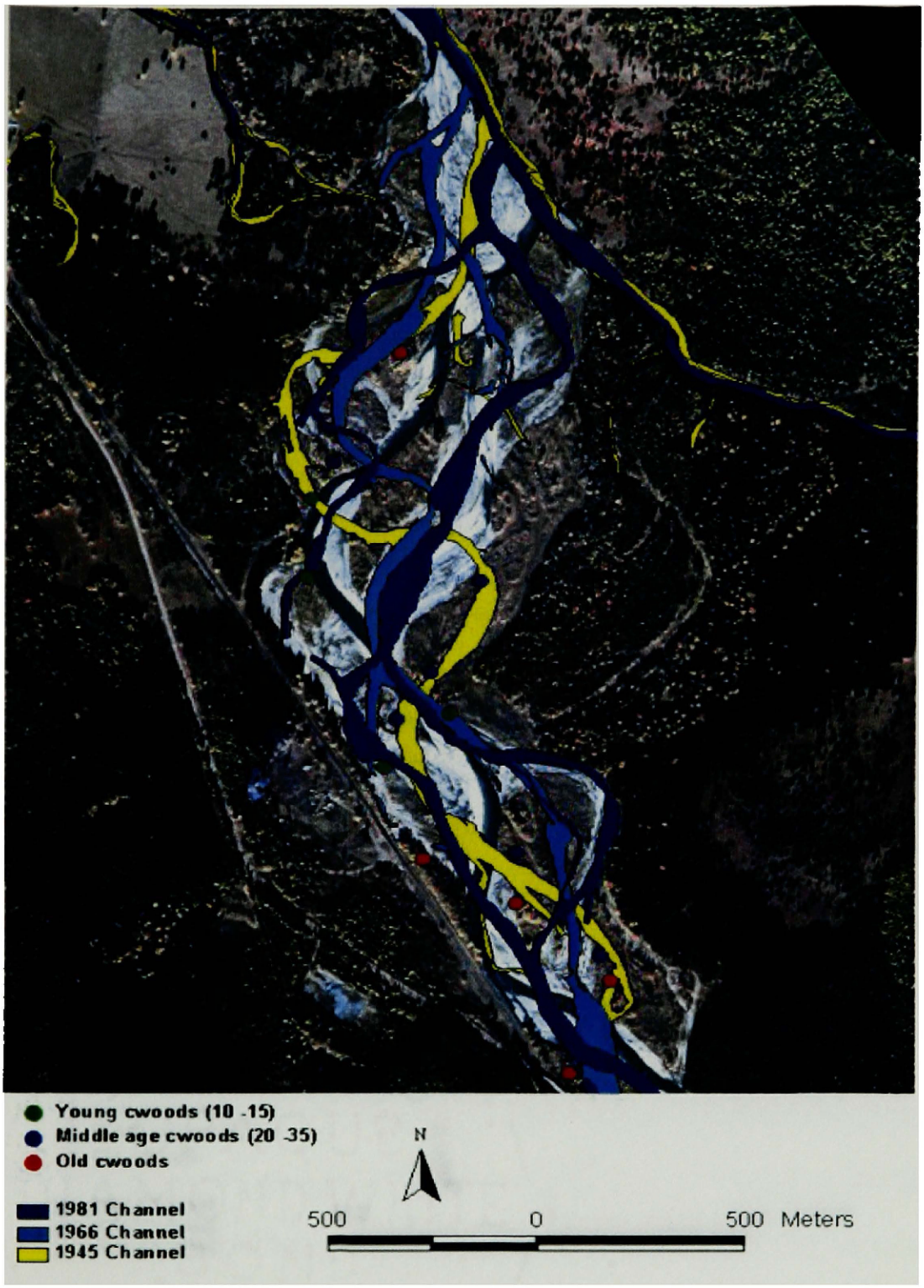


Fig. 14. Location of cottonwood plots in the losing reach relative to historic river channels. The base image is a 1999 photo of Nyack. The positions of the river channels in 1945, 1966, and 1981 are highlighted. Dots show plot locations, and the colors correspond to stand age classes (young < 15 yrs, middle 20-35 yrs, old > 35yrs).

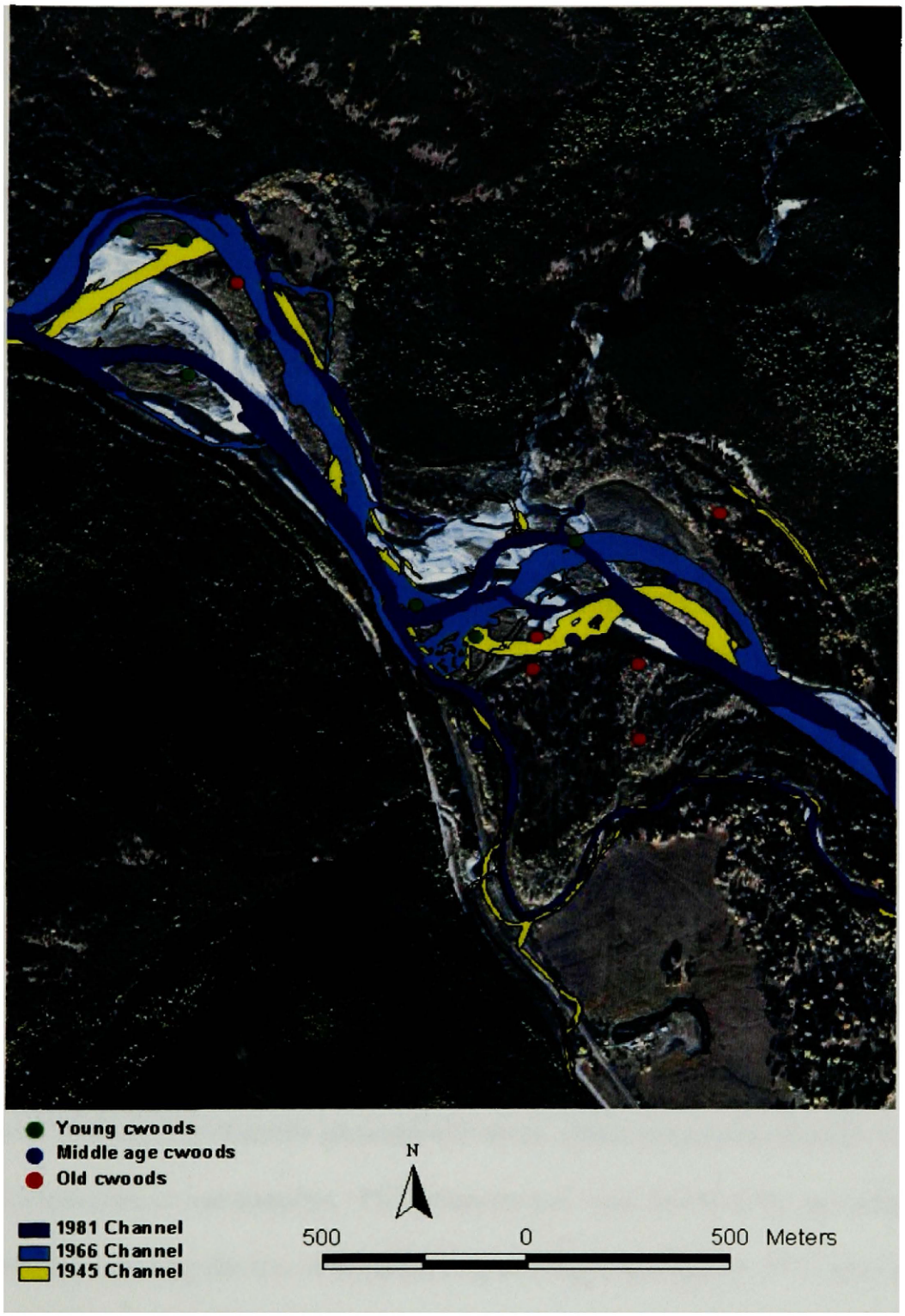


Fig. 15. Location of cottonwood plots in the gaining reach relative to historic river channels. The base image is a 1999 photo of Nyack. The positions of the river channels in 1945, 1966, and 1981 are highlighted. Dots show plot locations, and the colors correspond to stand age classes (young < 15 yrs, middle 20-35 yrs, old > 35yrs).

# Chapter 3

## Perspectives on the Study and Suggestions for Future Research

This study documented the influence of large-scale ($km^2$) patterns of down- and upwelling and hyporheic flow (Stanford and Ward 1988, 1993) on cottonwoods trees, which are an important riparian species that grow along rivers throughout north temperate latitudes. From a relationship between tree age and tree diameter, indices of growth rate were calculated and compared to site variables, such as depth to water table, stand density, and elevation above base flow. Considering the variability in biophysical processes of a large flood plain, the logistics of a field study on a dynamic river system like the Middle Fork, and the complications of cottonwood tree ring studies, the results of this study were insightful. However, hindsight led to some suggestions for future studies.

*Field work*

Characterization of flood plain water table dynamics was a challenging part of the study. Within reaches, change in ground water stage was measured within piezometers that were installed in the riparian forest. While this was an unconventional placement of piezometers, it worked to describe groundwater stage where placement of wells would have been expensive or not possible. PVC piezometers were installed by encasing them with a metal pipe, hitting the top of the pipe with a sledge, holding the PVC pipe in place, and removing the outer metal casing. The inexpensive material of the piezometers permitted them to be left in the field for repeated measurements, while the metal casing made it possible to drive the piezometers into cobble substrates. The piezometers did not

clog, except in 2 locations in the gaining reach. Early in the summer, wildlife removed three of the piezometers from the ground. There were also signs of chewing around the tops of three piezometers. Ground water was accessible in most piezometers through July, but some dried earlier. Using PVC piezometers is recommended where installation of wells is not possible.

Extracting increment cores from cottonwoods was not as difficult as had been anticipated. A large borer with a ½ inch bit was used to remove cores. The ½ diameter provided a large surface area to view rings for counting. In the field, cores were stored in wooden racks to protect the cores and to prevent the wood from bending as it dried. This worked well, except the racks were awkward to carry while hiking. The wooden racks were frequently wet from rain and water in the raft, so I recommend using strong wood when constructing the racks for storage. For another study later in the season, a smaller bit borer was used on cottonwood trees. This borer was easier to turn, and cores were stored conveniently in drinking straws. After sanding, I was able to count rings on the small cores as well as on the larger cores. However, the smaller cores came from trees growing in Washington where growth rates were much faster than in Montana. The smaller cores may have been difficult to read on slow growing trees. In terms of taking the cores, the only difficulty occurred on the lower flood plain near the outflow of Harrison Creek. The inner wood of these cottonwoods seemed rotten, even on trees with small diameters. The wood crumbled, spun, and clogged the borer. Intact cores were not extractable from most of these trees, and in some trees the borer stuck in the trunk. These trees had the symptoms "wet wood," such as stained and water soaked heartwood and branch dieback (Hofstra et al. 1999). A plant pathologist at Arizona State said that the

vector that causes wet wood is not known (J. Stutz, personal communication). I caution that extensive tree coring without sterilization due to the potential to infect the trees. An alternative to coring would be to measure branch increment growth, as studies show this is a sensitive indicator of water relations. (Willms et al. 1998, Scott et al. 1999). However, branch growth increments only provide 1 or 2 decades of tree information, thus limiting the time scale of the study (Willms et al. 1998).

Characterizing site variables was difficult because of complications associated with repeatedly reaching the plots, which was done by raft through the field season. Most measurements were direct, such as stem counts and diameter measurements. As expected, the soil characterization was rough, and would have been much more descriptive had thorough pit characterizations been completed. Understory composition was only generally classified. A study that compared site productivity and species composition to both soil textures (Merigliano 1996) and ground water might clarify the variation observed. I would also suggest installing 3-5 piezometers in each plot for ground water stage measurements.

While a direct methodology, surveying on the flood plain was difficult due to dense vegetation and frequent river crossings. The use of a laser theodolite expedited the work, as did back-sighting to Lone Man Mountain. While this is not as exact as back-sighting to a target, it reduced the difficult river crossings otherwise necessary to locate positions. The land surveys were conducted over a number of weeks with both a laser theodolite and an auto-level, so organizing the data sets from numerous files was time consuming. I recommend surveying in consecutive days with one surveying method. A sampling design that considered survey access would also be more efficient.

*Sampling design*

In designing this study, I was concerned about accurately measuring tree age. To overcome the variability associated with ring counting in cottonwoods, I sampled a large number of trees per plot, averaged the values within plots, and considered plots as the sample unit. With confidence, stand age was estimated. Other site variables were also characterized within a set area. However, this was a lot of work a few data points. An alternative sampling design would have been to sample fewer trees per plot, though even with sampling 15-20, there was a lot of variability in tree ages.

Perhaps a better method would be to use linear transects across the flood plain. With transects, piezometers could be placed in the channel and into the riparian forests so water patterns could be measured in relation to each tree, laterally from the channel, and longitudinally down the river corridor. To account for density, trees within a given radius of the sampled tree could be measured. Linear transects would also make topographic surveys more direct.

Another source of variability in the study came from not knowing the exact transition zones from down to upwelling on the flood plain. This was particularly complicated in the upper flood plain where a local gradient of down-upwelling occurred within a 1.5 km reach (Mouw et al. 2001). Some plots that were considered losing reach plots, may actually have been within a local area of upwelling. Transects across the flood plain with piezometer measures in the channel would have helped to clarify these patterns.

Coring trees in a neutral hydrologic region would help to clarify if growth differences are positive or negative responses to site variables. However, this is difficult

because data on the location of neutral zones in unclear, and these areas may be neutral at some times of the year and not others. Generally, this neutral zone occurs in the middle flood plain reach where logging and grazing occur. The understory in this area is further altered by grass planting and stand thinning to provide forage for cattle (J. Dalimata personal communication), so cottonwood stands are altered by human influences.

*Contributions to broader studies*

The study of the growth and distribution of cottonwoods on Nyack Flood Plain contributes to on-going and future studies of the biocomplexity of large riverine flood plains. This study, along with Mouw et al. (2001), demonstrates that the productivity and distribution of vegetation are influenced by the hydrologic variation and associated biophysical processes of large alluvial flood plains. Furthermore, the collection of field data provides biological data for use in image classification, such as stand density, canopy cover, and plot age. Also with the assistance of D. Whited, digitized photo series from 1945, 1966, 1981, and 1999 are available for future studies, as are the topographic surveys. An estimate of the age and stand distribution of cottonwoods is now available for an unregulated river, which will provide a comparison for work on regulated rivers, such as on-going work on the Yakima River by J. Braatne (University of Washington). The methods and base-line data from this study also contribute the Reaches study funded by the Bureau of Reclamation in Yakima, Washington. Using similar methodologies to age cottonwood trees, I assisted K. Clark (Central Washington University, MS student) and Dr. Mark Lorang (FLBS) with aging cottonwood trees on a gravel pit that has been

naturally reclaimed by the Yakima River. This provides an example of how cottonwoods can also serve as indicators of paleo hydrology.

*Future research*

This study only begins to capture the variation between the losing and gaining reaches. In terms of cottonwood structure, the gaining reach seems to generally have old or very young trees, with considerably fewer pole stands. Stands are also less homogenous and contain willow, alders, birch, and a number of understory plants. At the upstream end of gravel bars and in losing reaches, cottonwoods set buds and dropped leaves approximately 2 ½ weeks earlier than in other areas. I also observed more herbivore use of cottonwoods in upwelling areas, particularly downstream of Movie Road near the outflow of Nyack Creek (between plots 11 and 12, Chapter 2, Fig. 2). By early July, young trees (approximately 10 years) had damaged leaves and galls. Caterpillars were also common on the trunks of the trees in the gaining reach (around plots 17 and 18, Chapter 2, Fig. 3) and near the outflow of Nyack Creek. In plots about ½ km downstream of the upper floodplain knick point (Plots 22 and 23, Chapter 2, Fig. 2), numerous ants occurred on the buds, particularly around mid-late July. Beaver cutting was extensive around plot 12 (Fig. 2) and plot 19 (Fig. 3). Herbivore damage was not as common in the Red Eagle area among trees of the same age (10 years). Tolerance mechanisms, such as those presented by Coley et al. (1985) may explain this pattern. Perhaps trees in the strongly downwelling area (low-resource environment) may allocate more resources to defense because of the cost for them to replace damaged tissue.

Alternatively, genetics may play a role in the herbivore selection and/or plant resistance (Whitham et al. 1999).

In the proposal for this study, I hypothesized that plots in the upper and lower floodplain reaches would have fewer cohorts of trees than the middle reach, due to increased habitat complexity and the transitional nature of the braided reach. I also predicted that there would be more age classes in groundwater upwelling versus downwelling areas because upwelling areas are less prone to drought following decreased surface flows. My alternative hypothesis was that increased deposition at the lower flood plain (zone of general upwelling) may lead to fewer age classes due to stress from stem burial from sediments and/or intolerance to increased soil saturation and subsequent competition from willows. Because I did not pursue this study as a population structure study, I cannot comment on this with statistical support. However, it appears that the upper, active reach around Red Eagle (just below the upper knick point) and the area between Beaver Creek and the main channel in the middle reach have the greatest number of cottonwood cohorts. Possibly prolonged inundation and less channel movement in the lower reach leads to less recruitment. When trees do establish there, they do well, but optimal recruitment events may not happen as often.

The influence of floodplain geomorphology on asexual versus sexual tree reproduction, and hence population structure, would be an interesting avenue to pursue. Sex ratios (see Braatne et al. 1996) may be skewed in some reaches due to water and/or nutrient availability. Furthermore, studies are beginning to show the immense influence of genetic structure of cottonwood trees and how this extends to the entire food web (Kearsley and Whitham 1997, Waltz and Whitham 1997, Martinsen et al. 1998, Whitham

et al. 1999). For example, even on the same tree, leaves have different insect assemblages depending on phenolic contents (Waltz and Whitham 1997). Additionally, since cottonwoods are prolific clonal reproducers (Brayshaw 1965, Gom and Rood 1999) patterns of asexual reproduction likely influence the distribution of cottonwoods on Nyack. In this study, sexually versus asexually developed trees were not differentiated. A combination of studies of plant genetics and excavation of trees could be used to determine the kind of reproduction. I would hypothesize that there would be increased sexual reproduction (seeds landing on exposed sites) in zones of high erosion (like upper reach) and increased asexual reproduction in depositional zones because along with sediment, wood, which often re-sprouts, would be deposited in these regions. Another explanation for increased growth of some trees might be that if these sprouted from roots or buried stumps, they would have an additional source of nutrients.

Because of cottonwood contributions to ecosystems both as a living and dead specimens, their loss due to disruption of natural river flows will have far reaching consequences within river ecosystems. Future studies should consider vegetation productivity and diversity in relation to groundwater routing and residence time. Additionally, research on how rhizosphere exchange processes, such as those mediated by fungal hyphae, affect the chemistry of hyporheic water chemistries would further show how the surrounding landscape affects, and is influenced by, groundwater flow.

## Literature Cited


Braatne, J.H., S.B. Rood, and P.E. Heilman. 1996. Life history, ecology, and conservation of riparian cottonwoods in North America. *In* Biology or *Populus* and its implications for management and conservation. Part I, Chapter 3. *Edited by* R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman, and T.M. Hinckley. NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada. pp. 57-85.

Brayshaw, T.C. 1965. The status of the black cottonwood (*Populus trichocarpa* Torrey and Gray). Canadian Field-Naturalist 79:91-95.

Coley, P.D., J.P. Bryant, and F.S. Chapin III. 1985. Resource availability and plant antiherbivore defense. Science 230:895-899.

Gom, L.A. and S.B. Rood. 1999. Patterns of clonal occurance in a mature cottonwood grove along the Oldman River, Alberta. Canadian Journal of Botany 77:1095-1105.

Hofstra, T.S., J.C. Stromberg, and J.C. Stutz. 1999. Factors associated with wetwood intensity of *Populus fremontii* (Fremont cottonwood) in Arizona. Great Basin Naturalist 59:85-91.

Kearsley, M.J. and T.G. Whitham. 1997. The developmental stream of cottonwoods affects ramet growth and resistance to galling aphids. Ecology 79:178-191.

Martinsen, G.D., E.M. Driebe, and T.G. Whitham. 1998. Indirect interactions mediated by changing plant chemistry: beaver browsing benefits beetles. Ecology 79: 192-200.

Merigliano, M.F. 1996. Ecology and management of the South Fork Snake River cottonwood forest. Idaho BLM Technical Bulletin 96-9.

Mouw J. et al. 2001 *In review*. Local influence to vascular plant diversity on floodplain landscapes: attaining an ecosystem perspective.

Scott, M.L., P.B. Shafroth, and G.T. Auble. 1999. Responses of riparian cottonwoods to alluvial water table declines. Environmental Management 23:347-358.

Stanford, J.A. and J.V. Ward. 1988. The hyporheic habitat of river ecosystems. Nature 335:64-66.

Stanford, J.A., and J.V. Ward. 1993. An ecosystem perspective of alluvial rivers: connectivity and the hyporheic corridor. Journal of the North American Benthological Society 12:48-60.

Whitham, T.G., G.D. Martinsen, K.D. Floate, H.S. Dungey, B.M. Potts, and P. Keim. 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. Ecology: 80: 416-428.

Willms, J., S.B. Rood, W. Willms, and M. Tyree. 1998. Branch growth of riparian cottonwoods: a hydrologically sensitive dendrochronological tool. Trees 12:215-223.